

FOSSIL MAMMALS OF AFRICA

No. 20

FOSSIL ANTILOPINI OF EAST AFRICA

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SYNOPSIS

Up to five or even more gazelline antelopes are known from Beds I and II at Olduvai Gorge, Tanganyika, but only two of them can be assigned to named species—these are *Phenacotragus recki* (Schwarz) and *Gazella wellsi* Cooke. Both these forms are more closely related to the South African springbok, *Antidorcas marsupialis* (Zimmermann) than to typical gazelles, but less well preserved fossils at Olduvai belong to *Gazella* and are not related to the springbok. It is suggested that *Aepyceros* Sundevall be removed from the Antilopini to the Alcelaphini.

I. INTRODUCTION

OLDUVAI Gorge is in the Serengeti Plains of North West Tanganyika near latitude 3° S. and longitude 35° E. A revised account of the stratigraphy and palaeontology has been published by Leakey (1965); all that need be said here is that four beds, mostly arising from deposition in a lake or lakes, are present above a basaltic lava flow in the bottom of the gorge. On the basis of faunal correlations and potassium argon dating, Bed I is most likely to be contemporary with the Upper Villafranchian (Lower Pleistocene) of Eurasia. The transition from Bed I to lower II does not involve so great a faunal change as that between the lower and the upper parts of Bed II; above this latter break the Olduvai beds appear to belong to the Middle Pleistocene. The gorge itself was formed fairly recently, and the fossils dealt with here are practically all from living floors of Beds I and II.

The digging sites are referred to by combinations of initials, e.g. SHK, BK, FLK. At any site excavations may have been made at a number of horizontal levels, and

these are indicated by arabic numerals following the roman numeral for the bed. In a sequence of site layers within a single bed, lower numbers are later in time than higher numbers, which is the reverse of the method used in numbering the beds themselves. The layers 1-5 of site FLKN I excavated in 1960 are just below the top of Bed I and some 20 feet higher than site FLK (Leakey 1960). The fauna of FLKN I appears to show a drier climate than at the earlier sites. The age of FLK I is about 1.75 million years, and estimates nearer the top of Bed I were 1.02, 1.13 and 1.38 million years (Leakey, Evernden & Curtis 1961). A reference on a fossil to several layers, e.g. "layers 1-2-3" indicates that there had been a fall of the layers caused by a storm during excavation, so that the original layer from which the fossil came is unknown. Excavations at the sites SHK and BK in Bed II are in the upper part of that bed, that is after the major faunal change.

The fossils studied are in the National Museum's Centre for Prehistory and Palaeontology in Nairobi and the British Museum (Natural History), London. The latter collection contains fossils excavated until 1935, and the Nairobi collection those excavated thereafter. Specimens in the British Museum (Natural History) are referred to by their registered numbers and bed of origin, and those in Nairobi by their year of excavation and site number.

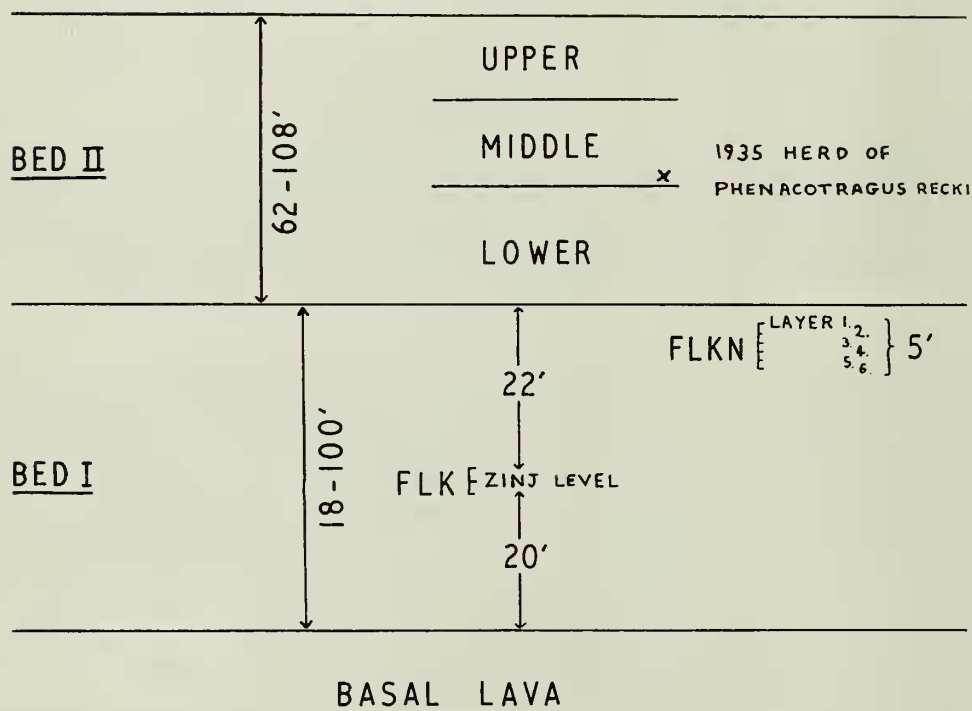


FIG. 1. Simplified diagram of Beds I and II, Olduvai Gorge.

Help and co-operation of various kinds have been received from numerous people, among them the following: in Oxford from Mr. H. K. Pusey my supervisor, Dr. A. J. Cain, and Dr. H. F. Lamprey; in Nairobi from Dr. L. S. B. Leakey and Mrs. S. C. Coryndon; at the British Museum (Natural History) from Dr. A. J. Sutcliffe, Dr. G. B. Corbet, Miss J. E. King and their staff; and during a short visit to Paris from Professor J. P. Lehman, Professor C. Arambourg, M. E. Heintz and staff of the Institut de Paléontologie. Dr. H. B. S. Cooke has kindly allowed me to see and refer to unpublished work on South African gazelline fossils. Most of the work was done in the Department of Zoology at Oxford on a research grant from the Department of Scientific and Industrial Research, and was submitted to the University as the greater part of a thesis.

II. GENERAL CONSIDERATIONS ON THE EVOLUTION OF GAZELLES

This paper deals with the tribe Antilopini, in which Simpson (1945) places six living genera other than *Gazella*. *Procapra* includes two or three Asian species which have frequently been assigned to *Gazella*. *Antidorcas* contains only one species, the well known springbok of South Africa, which does not range north of the Zambesi. *Litocranius* is the gerenuk of Somalia and East Africa characterized by its great shoulder height, an elongated neck, the long and massive occipital region of the skull, a brachyodont dentition and exceptionally shallow jaw rami. *Ammodorcas*, the dibatag, shares some characters with *Litocranius*, but its horns are forwardly curved from the base upwards, and it occurs only in restricted parts of Somalia. Little information is available on its ecology or on its ecological differences from *Litocranius*, with which it is sympatric and to which it is presumably closely related. Some notes on this rather mysterious animal are given by Meester (1960) and Schomber (1964). *Antilope* is the spiral horned blackbuck of India and *Aepyceros* is the impala which is very different from gazelles in face and coat coloration and in the shape of its horns. The females of most species of *Gazella* and of *Antidorcas* have horns, but in the other genera the females are hornless.

Among the fossil genera of Simpson's (1945) list, *Phenacotragus* is the one to which most attention will be given in this paper. *Dorcadoxa* from the Indian Pliocene consists of some frontlets and horn cores together with a "doubtfully referred" maxilla; Pilgrim (1939) thought these remains showed affinities with *Aepyceros* of East and South Africa. The other extinct genera, *Helicotragus*, *Protragelaphus*, *Gazellospira*, *Antilospira*, *Spirocerus* and *Dorcadoryx*, are all Eurasian spiral horned antelopes of Pliocene and Pleistocene age. Pilgrim looked upon them as having relationships with the living *Antilope*, and a review is given by Pilgrim & Schaub (1939).

The word "gazelle" in this paper is used as a noun or an adjective to refer only to the genera *Gazella* and *Procapra*, while "gazelline" refers to all the genera of Simpson's Antilopini including *Gazella* but excluding *Aepyceros*. The generic name "*Antidorcas*" or the English word "springbok" is used for the species *Antidorcas marsupialis*.

Definitions of the Antilopini and of *Gazella* have previously been given by Pilgrim (1939), Pilgrim & Hopwood (1928) and by Schlosser *in* Zittel (1925) as well as by earlier authors. Alterations and the addition of limb bone characters are proposed in the following definitions, and a definition of *Antidorcas marsupialis* is also given.

Tribe ANTILOPINI Simpson 1945

Small to medium sized antelopes with a moderately long face and braincase. Horn cores situated above the orbits or partly behind them. Horns of females smaller than in males or absent. There is a complicated suture between the frontals and parietal. The moderately long basioccipital does not narrow anteriorly except in some early forms. The face is little bent on the basicranial axis. The mastoid exposure of the periotic occupies a large surface area. An ethmoidal fissure is generally present between the nasal, maxillary, lachrymal and frontal bones. Most species have a small or medium sized preorbital fossa. Premaxillae are generally large and long. The infraorbital foramen lies above P^2 or P^3 when the skull is viewed with the tooth row in a horizontal position.

The molar teeth are brachydont in early forms but become hypsodont in many lineages. Basal pillars¹ on the inside of the upper molars and the outside of the lower molars disappear early in the evolution of the group. The enamel bordering the central cavities of the molar teeth shows little or no tendency towards a complicated pattern of folding. The premolars show relatively little advance in evolution towards molarization, and the central cavities of the upper ones are only rarely symmetrical; P_4 has an anteriorly closed medial wall only in some Asian *Gazella*.

The metapodials are long and their distal condyles have a large diameter. In the scapula the tuber scapulae comes well below the level of the glenoid facet in side view². In the humerus there is no projection of the bone backwards and outwards behind the infraspinatus insertion as a posterior eminence²; the great tuberosity is more or less upright and not curved over the bicipital groove, the top of the medial tuberosity is not drawn upwards to a prominent point and the distal condyles have large diameters. There is considerable twisting of the axis of the radius² and the posterior edge of the top medial facet is often indented. The articular area for the scaphoid on the posterior surface of the radius is short and narrows rapidly. The posterior surface of the shaft of the metacarpal is only slightly concave.³

The gluteus accessorius insertion on to the femur is situated low and forwards on the great trochanter; the cnemial crest of the tibia does not grade smoothly into the shaft below but instead has a distinct lower end. On the metatarsal there is only a poorly shown groove running down the anterior surface, the naviculo-cuboid facet becomes smaller in comparison with the ectocuneiform facet during the history of the tribe, there is no ridge bounding the lateral extensor tendon medially at the

¹ Basal pillars lie between the anterior and posterior lobes of the molar teeth.

² Not in *Antilope*.

³ Metacarpals assigned to *Gazella capricornis* in the British Museum (Natural History) have a deeply hollowed posterior surface.

top of the anterior surface, and the paired flanges towards the distal end of the anterior surface are prominent. A non-osteological character which is not useful in palaeontology is that the face often has a characteristic pattern of longitudinal dark and light striping. Most of the living species of Antilopini inhabit dry regions of the world and what observations there are suggest that they are facultative non-drinkers.

GAZELLA Blainville 1816

The horn cores have a sub-circular or elliptical cross section, their lateral surface is often flatter than the medial one and they have no torsion of their axes. In anterior view they are sub-parallel or divergent from one another; in lateral view they have a backward curvature which may take the form of a sudden, almost angular change of direction in some species. The females generally have horns which, when present, are set more obliquely than in males of the same species. Supraorbital foramina are situated in triangular-shaped depressions of the frontals—here called supraorbital pits—at the base of the horn pedicels. These pits are usually slightly on the medial side of the antero-posterior long axis of the pedicels. The level of the frontals between the horn bases is no higher or is only slightly higher than the level of the orbital rims. There are moderate to large sized auditory bullae. The premaxillae generally contact the sides of the nasals. The nasals have shortened in the evolution of the genus.

All living species have hypsodont teeth. The wall of the upper molars has three narrow vertical folds situated anteriorly, posteriorly and in the centre (parastyle, metastyle and mesostyle) as in many other Bovidae, but the two outwardly-bowed vertical swellings of the wall between the three styles are not prominent. The *pli caprin*⁴ of the lower molars is less marked than in some Caprine genera. *P*₄ originally has a medial wall with an open anterior valley and two small posterior indentations between three pillars, but in most evolutionary lines the posterior valleys close up leaving only the anterior valley open.

The edge of the ectocuneiform facet at the top of the metatarsal is usually more upcurved in side view than in other genera.

There are typically two teats but sometimes four, inguinal glands, well-developed pedal glands, carpal glands and preorbital glands (Pocock 1910, 1918).

ANTIDORCAS Sundevall 1847

Antidorcas marsupialis (Zimmermann)

(Pls. 4A, 9B, C)

DESCRIPTION. The horn cores are little compressed, without flattening of the lateral surface. In anterior view they are nearly parallel at the base and then diverge outwards as they bend backwards. The horns of females are sometimes

⁴ The *pli caprin* is a transverse expansion of the most anterior part of the lower molars separately from the main mass of the anterior lobe. It is best shown in some Caprine genera, also in *Gazellospira* and in lower teeth in the British Museum (Natural History) assigned to *Helicotragus* (Pilgrim & Hopwood 1928). In the present paper it will be called the goat fold.

more massive than in *Gazella*. Fewer individuals have a complicated frontals/parietal suture, and those with it have it less turned forwards in the centre. The supra-orbital pits are small and the frontals between the horn bases are at a higher level than the orbital rims. The braincase is shortened; the ethmoidal fissure very small or absent; the preorbital fossa small; the premaxillae reach the sides of the nasals; and the nasals are long with very pronounced central anterior flanges. The auditory bullae are small; the back of the basisphenoid is wide and its paired descending flanges originate at the back of the foramina ovals—more posteriorly than in *Gazella*. The palatal foramina may be set more posteriorly than in *Gazella*, and the hollow behind the maxillary flanges is deeper than in *Gazella*. The lower edge of the mandibular ramus rises rather steeply under the premolars from its great depth under the molars. The styles of the upper molars may be more pronounced than in *Gazella*; the lower molars have straight medial walls with anterior inturnings; the premolar row is very reduced. According to Pocock (1910, 1918) and Shortridge (1934) there are four teats, no inguinal glands, well developed pedal glands, no carpal glands, preorbital glands and a large dorsal gland on the back.

Fossil history of gazelles

In order to understand the gazelline remains of Olduvai, it is first necessary to consider briefly the history of gazelles and some of the characters used in their classification.

Gazella is first recorded in fossil form as the horn cores of *G. stehlini* in the European Upper Vindobonian; according to Thenius (1951) it was a large species. *G. pregaudryi*, from Oued Hamman in Algeria, may also date from the upper part of the Miocene (Arambourg 1959). By Pontian (Lower Pliocene) times gazelles had become abundant in the faunas of Asia and the more southerly parts of Europe. Kurtén (1952) has clearly separated brachyodont and relatively hypsodont gazelles in China, but he did not consider how the Chinese species might be related to those of Europe. The best grounded Pontian species of Europe are:

1. *G. deperdita* from Cucuron, Mount Léberon and other sites, with slight lateral compression of its horn cores which are also slightly flattened on their lateral surface. Towards the tip they diverge outwards.

2. *G. capricornis* known principally from Pikermi in Attica. The horn cores are less compressed than in *G. deperdita* and have no flattening of the lateral surface. It may be noted now that flattening of the lateral surface of the horn core and degree of lateral compression are independent characters in gazelles; it is not necessary that lateral compression be accompanied by a less convex lateral surface, and descriptive phrases such as "of circular (or non-circular) section" are not always clear.

3. *G. pilgrimi* (formerly *G. gaudryi*) from Samos has horn cores with a flattened lateral surface and a small degree of lateral compression but they differ from *G. deperdita* in the more regularly elliptical shape of their cross section and in being less blunt and not outwardly divergent at the tips. The premolar row is relatively shorter than in *G. capricornis*.

4. *G. mytilinii* is a larger species from Samos with distinctive lower teeth, if

those in the British Museum (Natural History) are correctly associated with the horn cores.

The best known gazelles of the later Pliocene are those from China, for example *G. blacki*.

G. borbonica from the Villafranchian (Lower Pleistocene) of Europe is about the size of the living East African *G. thomsoni* and very similar in appearance with its compressed horn core of nearly symmetrical cross section. The closest Pontian type of horn core would have been that of *G. pilgrimi* which is less compressed, but no relationship has been proved. The so-called *G. anglica* of the East Anglian Craggs is probably the same species as *G. borbonica* and shows how gazelles had by then spread northwards. The contemporary *G. sinensis* of China is totally unlike *G. borbonica* and has large thick horn cores.

Pleistocene gazelles are common in Africa, and Arambourg (1957) recorded two extinct Upper Pleistocene species in North West Africa which are named *G. atlantica* and *G. tingitana*. The former has short, not very compressed horn cores which curve gently backwards and seem to stand between those of *G. desperdita* and *G. sinensis* in general appearance, although measurements show that they are actually less compressed than in either of these species. *G. tingitana* has very long, slender, curved horn cores without much resemblance to any other gazelle except just possibly to some of the horn cores from the Palestine Natufian levels assigned by Bate (1940) to *G. decora*, e.g. the horn core (M.16347) in the British Museum (Natural History). In South Africa one finds *G. wellsi*, a species to be considered in the next section. *G. gracilior* (Wells & Cooke 1956) is a small South African species with fairly steeply inserted horn cores which are less compressed than those of living African species. The name *G. praethomsoni* has been given to a horn core, a fragment of a mandible and a metatarsal from Omo in South Ethiopia (see Arambourg 1947). The horn core does not look unlike illustrations of *G. gracilior*, and is similarly less laterally compressed than in living species. Dietrich (1950) worked on gazelle material collected by Kohl Larsen's 1935 expedition to the Laetoli area near Olduvai; he separated teeth into three groups called *G. kohllarseni* (the largest), *G. janenschi* (the size of *G. thomsoni*), and *G. hennigi* (the smallest). Horn cores were found but appear in only one of the figures.

Fossil teeth referable to *Antidorcas* have been found in South Africa (Cooke 1963), but Arambourg's (1947) *Antidorcas* sp. from Omo does not appear to belong to this genus.

Characters used in the classification of gazelles

Gazelle horn cores thus show great variation of shape (compressed or not, flattened lateral surface or not), insertion (divergent or not in anterior view, rising steeply or obliquely from the frontals), and course (degree of backward curvature, outward divergence of the tips, sudden or gradual changes in course). Among the later types one could separate as two extremes the short, robust type of *G. sinensis* (with *G. atlantica* lying near to it), and the long, compressed, more nearly symmetrical type of *G. borbonica*. *G. pilgrimi*, *G. gracilior* and *G. praethomsoni* look more like *G.*

borbonica but are less compressed, while *G. capricornis* and *G. pregaudryi* are also quite unlike the *G. sinensis* type but are so little compressed as to be almost circular in cross section. The evolutionary relationship of these forms has not been worked out, nor has their history been brought into relationship with the evolutionary changes in the teeth. The most compressed horn cores appear later in the record, and presumably they and the *G. sinensis/atlantica* type could be traced back to an ancestral condition like *G. capricornis* or perhaps to a type intermediate between *G. capricornis* and *G. deperdita*. Despite their great intraspecific variability horn cores are undoubtedly the most useful fossil remains for classifying extinct gazelles, but one cannot assume that horn core similarity is a reliable indicator of phylogenetic relationship.

Various opinions have been held on the history of horns in female gazelles. The evidence is slender but it seems likely that they were already present in early forms as is supposed in *G. stehlini* (Thenius 1951) and that their disappearance is secondary. Hence *G. thomsoni* would be the most advanced living African gazelle for this character, for the females' horns are certainly small and most variable in direction and insertion as would be expected in an organ about to disappear. According to Pilgrim (1937) *G. lydekkeri* from the Dhok Pathan (Middle-Upper Pliocene) of India already had hornless females.

Concerning other skull characters of the genus, Pilgrim (1939) recognized that nasals are proportionately longer in the earlier species and this is borne out by measurement on a skull of *G. capricornis* in Paris in which the nasals were 6.34 cm long and 2.15 cm. wide. Taking width as a percentage of length gives a value of 34%, whereas estimates for the living *G. dorcas* and *G. thomsoni* have means of 46 and 58.5 respectively (Gentry 1964). The basioccipital of a *G. capricornis* skull in London (M.11440) and of a *G. deperdita* in Paris were short and relatively more narrow anteriorly than in living gazelles and were thus somewhat nearer to the condition of other early Boridae.

The character of the low level of the frontals between the bases of the horn is not different in the Pontian gazelles from those now living and is also found in the related genera *Oioceros*, *Helicotragus*, *Antilope*, *Litocranius* and *Ammodorcas*. The supra-orbital pits of Pontian gazelles and of *Ammodorcas* and *Litocranius* are smaller than in living gazelle species but share with them the typical triangular shape around the foramina. The combination of triangular pits and low level frontals give this region of the skull its characteristic appearance in males of these genera (Plate 9A). *Antidorcas* on the other hand has frontals at a high level between the horn pedicels, and its small supraorbital pits, hardly distinguishable from the foramina they surround, are long ovals and not triangular in shape. It is thus likely that in Antilopini the size and shape of the supraorbital pits are at least partly correlated with the level of the frontals, if not entirely so.

The teeth of gazelles

In Pilgrim's opinion (1939 : 31) the teeth of the early gazelles are not far removed from the original Bovid condition, and the genus retains a relatively primitive tooth

structure throughout its history. However some evolutionary changes do occur, for instance: diminution of the basal pillars (in early gazelles these lie between the anterior and posterior lobes of the molar teeth on the inner side of the uppers and the outer side of the lowers), increasing hypsodonty, and an increasing depth of the mandibular ramus to house the longer teeth. The reason for the decline of the basal pillars (they may be retained in other groups such as the Reduncini and Bovini) is not easily understandable, but the other changes are obvious improvements of masticatory efficiency.

But these modifications within *Gazella* are not so pronounced as those which occur in other gazelline genera and in the closely related Caprinae. The list of possible changes is:

1. Little worn upper and lower molars come to possess transverse ridges across the anterior and posterior lobes. These ridges are seen on the dentine as well as on the enamel.
2. Accentuation of the styles on the outer walls of the upper molars.
3. A flattening of the outer walls of the upper molars between the styles. This may proceed to such an extent between the mesostyle and metastyle that the posterior outer surface becomes concave.

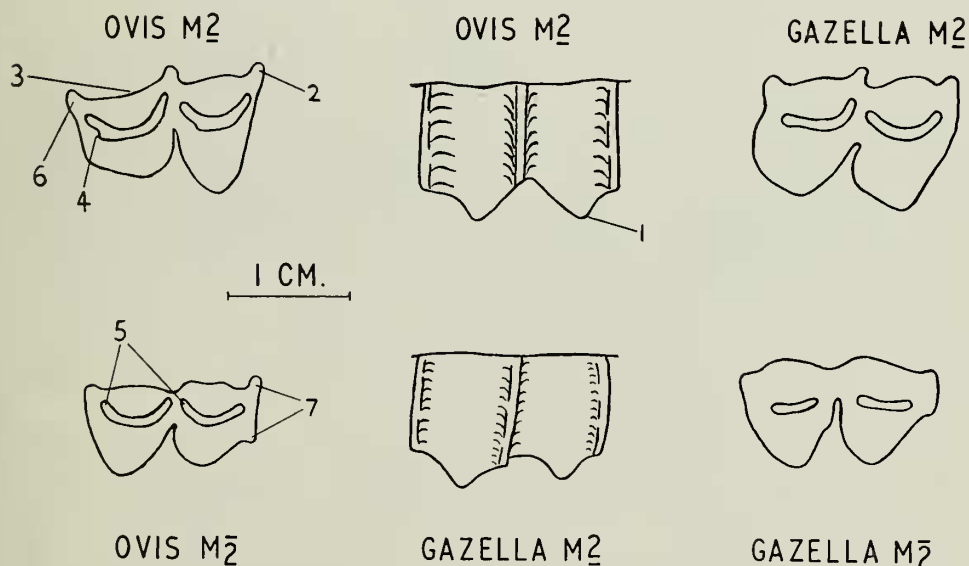


FIG. 2. Upper and lower molar teeth of a gazelle (*Gazella granti*) and a sheep (*Ovis aries*).

Occlusal views on the left and right, lateral views in the central column. The anterior side of every tooth is on the right; the lateral side of the upper molars is at the top and of the lower molars at the bottom. The numbers are those of the characters listed in the text. The shape of M^2 in *Ovis* with the anterior lobe being long and narrow and the posterior lobe short and wide is often found in Caprinae.

4. Increasingly complex course of the enamel wall around the central cavities of the anterior and posterior lobes of the upper molars: infoldings of the wall into the cavities appear.

5. The central cavities become longer and more curved, and they retain their symmetry better as they are worn down in life.

6. The metastyle of M^3 becomes a prominent flange.

7. Goat folds (see footnote on page 49) may develop on the lower molars.

8. The inner wall of P_4 is changed so as to make the tooth more like a molar.

9. The premolars may become so reduced that P^2 and P_2 , or either, disappear.

Characters 1, 2, 3, often 4, 5, 6, 7, and 8, of the above list are easily examined on the teeth of *Ovis* or *Capra* (Text-fig. 2). Since the transverse ridges, 1, affect the dentine as well as the enamel, their presence may be attributed to changed occlusional movements, in gazelles the dentine of the lobes is often scooped out. The strengthened styles, 2, of the upper teeth are more resistant to the tops of the transverse ridges of the lower teeth and can be regarded as a correlated character. The concavity of the posterior outer wall in the upper molars, 3, probably helps to prevent the tip of its transverse ridge being chipped. The goat folds of the lower teeth, 7, avoid the consequences of the transverse ridges of the uppers acting across the divisions between the successive lower molars.

One can see these changes, and the molarization of P_4 as parts of an improved masticating mechanism. Varying combinations of all eight of these changes may evolve in Antilopine genera other than *Gazella*, and, according to Pilgrim (1939: 19), "alongside *Gazella* at every geological stage precocious Gazelline types are met with". When these changes are pronounced and accompanied by other skull alterations there is difficulty in assigning the genera to the Antilopinae or the Caprinae. The explanation for the different structure of gazelle and caprine teeth may be that they are adapted to feeding in different ways. Alternatively it is possible that selection in gazelles may not have acted primarily in favour of dental efficiency so much as in favour of cursorial improvements in the legs and the physiological mechanism for drought resistance. It was pointed out to me in discussion that if this were true, then the teeth of gazelles ought to be more variable than those of sheep and goats; such variability has yet to be proved.

It appears not to be wholly correct to describe such changes as adaptations to grazing. Nobody has ever suggested that the Caprinae are more fully grazing animals than the Antilopini, and it has been pointed out (Zeuner 1963) that within the Caprinae *Capra* is in nature more of a browsing animal while *Ovis musimon* at least is a more thoroughgoing grazer. None the less the detailed morphology of the teeth appears identical in the two genera. Then again very little is reliably known of the feeding habits of gazelles, although Brooks (1961) found that a high percentage of grass is taken by the East African *G. thomsoni*. However he also found that this species is a fastidious eater when the opportunity allows and that it prefers fresh shoots of grass where burning has occurred, and according to Lamprey (1963) *G. thomsoni* likes short grass previously grazed by other ungulates. In fact ecological

research might still show that gazelles are better described as mixed feeders with a tendency towards grazing, than as predominantly grazers.

Characteristics of P_4 have often been used in the classification of gazelles and their relatives, and some authors refer to primitive and advanced patterns of design. What seems to happen is that the inner wall of P_4 in the older fossil gazelles such as *G. capricornis* is indented by an anterior and two posterior valleys as can be seen in Text-fig. 3 in *Litocranius* which shows the same characters. In gazelle evolution there is a tendency for the more posterior pillars of the medial wall to coalesce, which leaves a more or less flat inner wall behind the surviving anterior valley. This condition is seen in the living species *G. thomsoni*. Among the Antilopini as a whole the possession of at least two valleys on the internal side of P_4 is a mark of early forms or can be seen as a primitive character in living species. But, as is usual with so many Bovoid characters, there is much intraspecific variability and conclusions must be drawn with care. Some genera of Bovidae, but only the species *G. sinensis*, *G. gutturosa*, and *G. picticaudata* within *Gazella*, show a condition in which the anterior

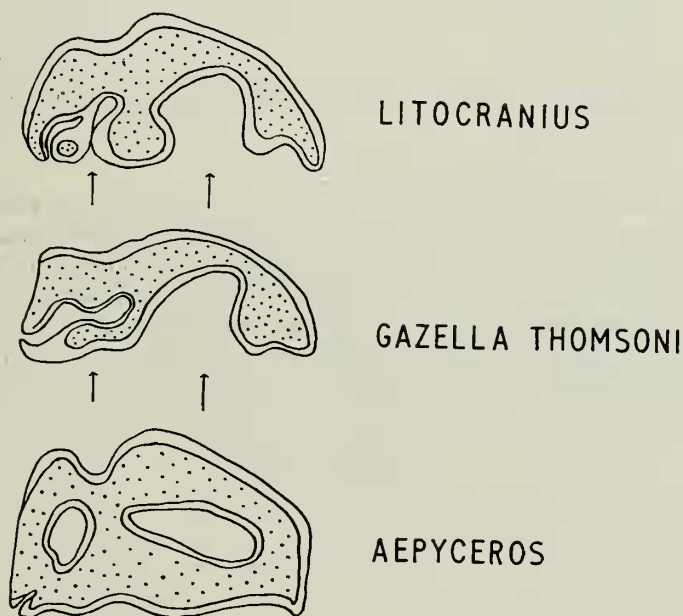


FIG. 3. Occlusal views of the left P_4 in three antelope genera. Not to scale.

The anterior side of each tooth is on the right and dots show where enamel has been worn away to expose dentine. *Litocranius* has anterior and posterior valleys on the medial side, shown by arrows; this is the condition found in early gazelles. In *Gazella thomsoni* the posterior valley has practically disappeared; this condition is found in later gazelles. It must also be noted that the posterior valley becomes more nearly closed up as individuals age, and that there is much intraspecific variation. In *Aepyceros* the anterior valley of the medial wall has closed up completely.

valley between metaconid and paraconid closes up as well as the posterior valley. The posterior part of the tooth shortens so that there is an almost entirely closed inner wall of P_4 formed from what would be the anterior part of the tooth in a gazelle. This character is clearly a move towards the molarization of P_4 , and gazelles can be considered as not advanced.

The condition of P_4 in some of the species and genera mentioned in this paper is shown in the table :

	State of P_4	<i>Gazella</i> species	Other genera
I.	Posterior part of internal wall still open	<i>capricornis</i>	<i>Litocranius</i> , <i>Ammodorcas</i>
II.	Posterior part of internal wall closed or becoming closed	<i>pilgrimi</i> , <i>deperdita</i> , <i>dorcas</i> , <i>spekei</i> , <i>granti</i> , <i>rufifrons</i> , <i>thomsoni</i>	<i>Phenacotragus</i> , <i>Antidorcas</i> , <i>Antilope</i>
III.	Anterior part of internal wall closed	<i>gutturosa</i> , <i>sinensis</i> , <i>picticaudata</i>	All genera of Caprinae ; <i>Aepyceros</i> , <i>Alcelaphus</i> , <i>Damaliscus</i>

Among the gazelle species in category II the ones with the most nearly closed valley are probably *G. thomsoni* and *G. rufifrons*.

III. FOSSIL GAZELLINE SPECIES AT OLDUVAI

The remains of five or six gazelline species from the Olduvai beds will be described, although only two of them are well enough preserved to be referred to named species. The better represented ones show no apparent signs of relationship to the present day East African *Gazella thomsoni* or to *G. rufifrons* (a West African species similar to *G. thomsoni*). The most frequently occurring fossil species, *G. wellsi*, has some characters which are not entirely dissimilar from *G. dorcas*, but a far more likely phyletic relationship lies with the South African springbok.

Gazella wellsi Cooke

(Pls. I, 2A, B)

1949 *Gazella wellsi* Cooke: 38, text-fig. 11.

MATERIAL

1960, FLK I, Gr3, 229	right horn core.
1960, ,, ,, 230	left horn core, presumably the same individual as 229.
1960, FLKN I, layer 5, 6334	crushed skull with horn cores and teeth. Plate IB.
1960, ,, ,, I, 1307	crushed skull with right horn core. Plate 1A.
1960, ,, ,, 5, no no.	crushed skull with worn teeth.

1935, DK I, B.M. (N.H.) M.22360	.	.	.	right horn core.
1959, HWK II, 471	.	.	.	base of left horn core with top part of orbital rim.
1959, ,, 473	.	.	.	right horn core.
1959, ,, 568	.	.	.	left horn core.
1960, FLKN I, layer 3, 1152	.	.	.	left upper dentition. Pl. 1C.
1960, ,, ,, 3, 618	.	.	.	incomplete right upper dentition.
1960, ,, ,, 1-2-3, 871	.	.	.	right P ³ -M ¹ .
1960, ,, no number	.	.	.	left M ¹ -M ³ .
1960, ,, layer 1-2-3, no no.	.	.	.	left M ² -M ³ .
1960, FLK I, Zinj. level G.323	.	.	.	right mandible. Pl. 2A.
1960, ,, ,, D.35	.	.	.	left mandible.
1960, ,, ,, G.294	.	.	.	right mandible. Pl. 2B.
1960, ,, ,, 492	.	.	.	left mandible.
1960, FLKN I, layer 1-2-3, 914	.	.	.	left mandible.
1960, ,, ,, 1-2-3, 935	.	.	.	right mandible.
1960, ,, ,, 1-2-3, 503	.	.	.	left mandible.

together with other fragments.

The size of the animal is about equal to that of the living Thomson's gazelle or slightly larger.

Horn cores

The horn core FLKN I, 1307 (Pl. 1A) which is probably from a male is robustly built. A short distance above the pedicel it bends backwards but does not diverge outwards, and then tapers quickly to a point. The medial surface is more rounded in section than the lateral surface and the horn core as a whole has little transverse compression. The diagram of the cross section (Text-fig. 7) also shows that while the anterior half is evenly rounded, posteriorly there is at least a tendency towards the development of a postero-lateral edge. Short and irregular longitudinal ridges and furrows are easily seen on the surface.

The two FLK I horn cores, nos. 229 and 230, are better preserved and more complete than the above specimen. They are less robust than 1307, have pronounced transverse ringing on the anterior surface, and are perhaps not quite so sharply bent backwards in their distal parts, but they have similar longitudinal ridges and furrows. Additional characters not observable on 1307 are that these horn cores do not rise very steeply from the frontals in lateral view, they are fairly strongly divergent from the base in anterior view (this character is to be distinguished from the outward bending of the distal parts alone which is seen in the *Phenacotragus* to be described later), the supraorbital foramina are set in small rather than large supra-orbital pits and the frontals between the horn bases are at a higher level than the orbital rims.

The horn cores of the skull FLKN I, 6334 are as slenderly built as 229 and 230 and definitely less sharply bent back than 1307. The lateral surface is more noticeably

flattened than in 1307, the longitudinal furrows are not so deep, and faint transverse ridging can be felt on the lower parts of the anterior surface. On account of the slenderness and smoothness of its horn cores, 6334 is most satisfactorily interpreted as a female of the same species as its contemporary 1307; this leaves open the sex of the FLK horn cores from earlier in Bed I, the maleness of which would not have been questioned had 6334 not been found.

Horn cores comparable to 1307 have been commonly found at Olduvai since 1931, but they have nearly all been surface finds. F.939, F.940, F.944 and F.946 are surface finds from Bed I in 1941. In the British Museum (Natural History) M.14511, M.22363 and M.22479 are also surface finds from Bed I, whilst M.21456 is a surface find from Bed II and M.14563 from Bed IV. In addition there is a cranium, M.21463, which was a surface find from FLK II in 1935, and has retained both horn cores, complete supraorbital pits and much of its basioccipital. It is evident then that these horn cores have a long temporal distribution at Olduvai, since the 1960 specimens are undoubtedly from Bed I while M.21456 and M.14563 cannot be earlier than Bed II and Bed IV respectively.

M.22360, excavated from Bed I at site DK in 1935, is not a surface find and it deviates markedly from the 1960 horn cores in being narrow anteriorly and, less markedly, in having a more prominent postero-external edge. It agrees with the horn cores described above in the oblique insertion and outward divergence, and in the small supraorbital pit. The horn cores within many species of living gazelles show a considerable variability of shape, so it is most probable that M.22360 is conspecific with the 1960 horn cores. The impression given by all these horn cores is of one species, or at the most a superspecies, showing all the variation one might expect among its populations inhabiting the changing environment down the ages.

Upper teeth

The crushed skull FLKN I, 6334, provides the essential link between the horn cores and the upper teeth of this species. The teeth of this, as of most of the other specimens of upper teeth, are well worn. The youngest complete set is FLKN I, 1152 (Pl. 1C) which is in age state IX according to Brooks' usage (see Appendix 1), while the fragment FLKN I, 871 has two recently erupted premolars. In addition there are some comparatively unworn isolated molars from FLKN I, and FLK I.

There may be a difference from living African gazelles in the more prominent flange formed by the metastyle of M³. When using this character it is essential to compare individuals of approximately the same age in different species, since the size of the metastyle increases in later life. Allowing for this age effect, one sees that *G. wellsi* may perhaps resemble Caprine genera and the Asian *Gazella picticaudata*, *G. gutturosa* and *G. subgutturosa* in this character rather than extant African gazelles. A number of isolated but unworn upper molars from FLKN I are probably assignable to this species; the styles may be slightly more pronounced than in living gazelles but certainty is impossible. Apart from this and the development of the metastyle of M³, the morphology of the teeth is like living gazelles.

The most startling feature of the upper dentition, however, is the extreme shortness

of the premolar row expressed as a percentage of the length of the molar row. The ratio can be determined on the skull 6334 and on the upper dentition 1152. Text-fig. 6 shows that the fossil premolar rows are as short as the shortest ones found in *G. thomsoni* which has the most reduced premolar row among living gazelle species in Africa, but it may be seen that the springbok has a still lower premolar/molar row ratio than the fossil, and it will be suggested that it is to *Antidorcas* and not to *Gazella* that *G. wellsi* may well be related. The actual statistics for the fossils and some living species were :

	Number Measured	Mean Value	Range	Standard Deviation
<i>G. thomsoni</i>	64	57.3	51-64	3.00
<i>G. rufifrons</i>	17	63.6	57-68	3.41
<i>G. dorcas</i>	31	63.4	58-69	3.17
<i>Antidorcas marsupialis</i> (with P ²)	9	47.8	46-52	1.85
(without P ²)	5	35.6	34-37	2.30
<i>G. wellsi</i> : c.50 ; 48 ; mean value : 49				
FLKN I, 1662 : 49				
<i>Phenacotragus recki</i> : c.56, 48, 59 ; mean value : 54.3				
<i>G. capricornis</i> : 75, 74 ; mean value : 74.5				

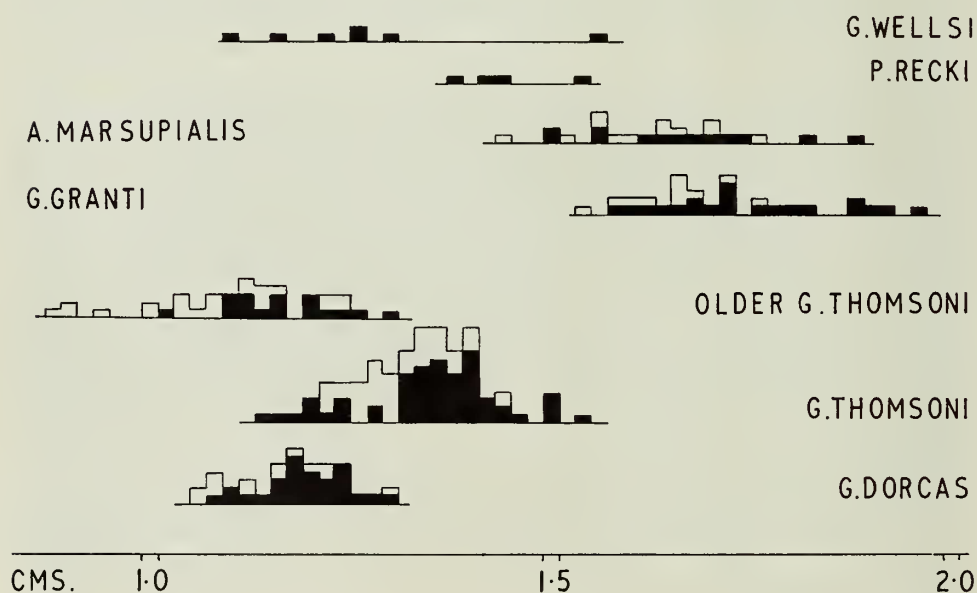
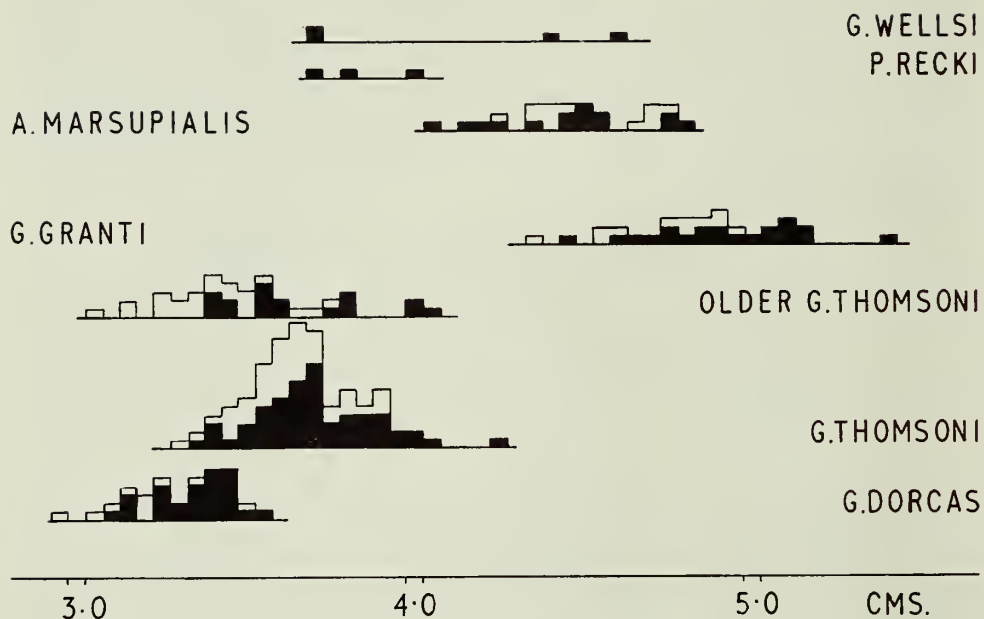
The confidence limits for the differences in mean values between the living gazelles were :

<i>G. thomsoni</i> - <i>G. dorcas</i>		6.1 ± 1.32 with 93 degrees of freedom
<i>G. thomsoni</i> - <i>G. rufifrons</i>		6.3 ± 1.68 with 79 degrees of freedom

The functional significance of the relative lengths of premolar and molar row is that longer molar rows are adaptive to grazing and perhaps to dust contamination of the grass eaten.

An upper dentition, FLKN I, layer 1, 1662 (Pl. 1C) is rather large but may belong to this species. Since the teeth are in age state X and since identification becomes more difficult with advancing age, there can be no certainty that it does not really belong to *Phenacotragus*. The styles on M² are slightly better developed than in the teeth of the other maxillae, but not so as to be beyond their possible range of variation. On the histogram of lengths of M¹-M³ (Text-fig. 4), 1662 just comes within the possible size range of *G. wellsi* providing that the other fossils are all smaller than average size. On Text-fig. 6 the length of its premolar row is 49% of the length of the molar row. If 1662 is not *Phenacotragus*, then it might belong to a larger species closely related to *G. wellsi*. There is also the possibility of size changes within *G. wellsi* over periods of time, but more numerous remains are required for an analysis.

Finally, turning from tooth characters, it may be noted that the back of the maxillary bone in 1152 has a lesser slope as it rises towards the zygomatic arch than in living gazelles and that the right maxilla of 6334 shows the presence of a preorbital fossa as in living gazelles. 1959, HWK II, 471 shows that the orbital rims were wide.



Mandibles

Unfortunately there is no associated find of a lower jaw with an upper jaw or horn core. The mandibles listed above are, however, assigned to this species because their size is right and because the premolar rows are as short as in the upper teeth. Six of the ten pieces come from FLK, and all ten have worn teeth. The character of overriding interest is the extent to which P_2 has been reduced. It is very small in FLK I, G.154 and in FLKN I, 976 and could hardly have been larger in FLK I, D.65 and, finally, in FLK I, G.294 (Pl. 2B) it is altogether absent. The elimination of P_2 occurs in Alcelaphini, and in *Antidorcas*, *Pelea*, *Antilope*, *Saiga* and *Pantholops* and its absence is not always invariable. It is therefore noteworthy to find such an advanced condition so long ago as in the early part of Bed I at Olduvai. The probability is, in both the fossil species and in the springbok, that the tooth disappears some time in adult life. It has been well established (Dekeyser & Derivot 1956) that upper canine teeth can occasionally be found in very young Bovidae although never in adults, hence it would be surprising if P_2 were not present in very many individuals of the springbok and *G. wellsi*, at least as a vestige after eruption of the permanent premolars.

Most of the fossil specimens are crushed, but it can be seen (Pl. 2A) that the ramus is deep below the teeth, even anteriorly where it may perhaps exceed the depth usual in living *G. thomsoni* which, with other living species, is deeper than in Pontian gazelles. This character, taken in conjunction with the reduction and loss of P_2 , suggests advanced grazing adaptations. The anterior edge of the ascending ramus is complete in FLK I, G.323 and it has a less abrupt slope than in *G. thomsoni*. This is in agreement with the slope of the back of the maxilla in FLKN I, 1152 and suggests that in these animals the tooth row as a whole lay rather forwards.

Comparisons

The first point to be made about this species is its obvious lack of relationship with the living gazelles of Africa, which I have considered in another paper (Gentry 1964). The shortness and sharp bending back of the distal parts of the horn cores and the

FIG. 4. Histogram of length of M^1 - M^3 .

The readings for the Recent species were taken on individuals in age states VIII and IX as explained in Appendix 1; the distribution for older *G. thomsoni* is for specimens in age state X and above, and shows the size decrease with advancing age. The reading on the extreme right of *G. wellsi* is FLKN I, 1662, including the metastyle flange of M^3 ; the reading to the left of it is of the same specimen excluding the flange. FLKN I, 1662 thus only just falls within the likely size range of the other two complete molar rows assigned to this species. It and FLKN 6334 are in age state X, while FLKN I, 1152 is in age state IX. Unblackened readings indicate females, blackened ones males in living species; all entries for fossils are blackened.

FIG. 5. Histogram of length of M^2 .

Older *G. thomsoni* in age state X and above are shown separately as in Fig. 4; here there is a definite decrease in length with advancing age, caused by the growth of M^3 . The reading on the right of *G. wellsi* is FLKN I, 1662. Unblackened readings indicate females, blackened ones males in living species; all readings for fossils are blackened.

slight transverse compression are not totally unlike the living *Gazella dama*, but in other respects there is no resemblance. The less reduced female horns are probably more primitive than in living species, but the teeth and lower jaws appear to be more specialized. On the whole it is less unlike *G. dorcas* than *G. thomsoni*; this is seen in such characters as the smaller supraorbital pits, the horn cores being bent backwards (although more sharply than in *G. dorcas*) and the comparative lack of transverse compression of the horn cores. (However, Text-fig. 7 shows that the widest part of the fossil horn core lies at a more anterior level than in *G. dorcas*.) These characters in the fossil are probably evidence for the view that *G. thomsoni* has evolved further from its ancestral condition, as far as they are concerned, rather than evidence for the fossil's relationship to *G. dorcas* in particular. The short premolar row is quite different from *G. dorcas*.

The species is not at all like *G. praethomsoni* from Omo (Arambourg 1947), which has a smaller horn core without a backward bend. *G. gazella praecursor* was described from Olduvai by Schwarz (1937). The type was not figured and so far as is known it was destroyed at Munich in 1944. The description speaks of hypsodont teeth and of horn cores being sharply bent back in their upper parts, but it also

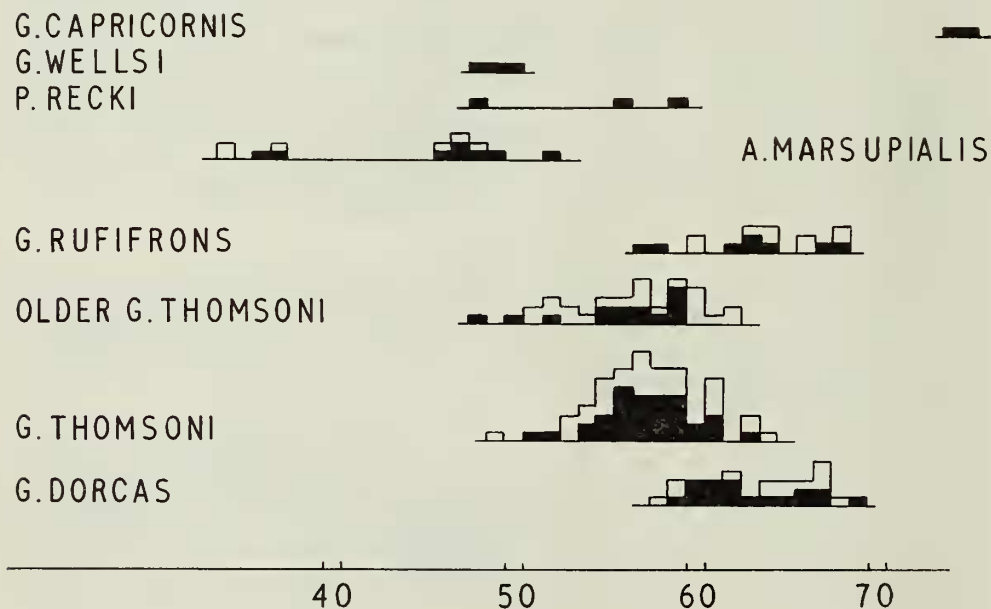


FIG. 6. Histogram of $(\text{length } P^2-P^1 / \text{length } M^1-M^3) \times 100$.

The group of *A. marsupialis* on the left are those without P^2 , those on the right have retained it. Note the difference between *G. thomsoni* and *G. rufifrons*. *G. capricornis* is the main Pontian gazelle from Attica. Unblackened readings indicate females, blackened ones males in living species; all entries for fossils are blackened.

mentions that the upper parts of the horn cores diverged outwards and that they were laterally compressed with a basal index of about 65 or more. This does not sound like the present species. The horn cores of *G. atlantica* of the Algerian Upper

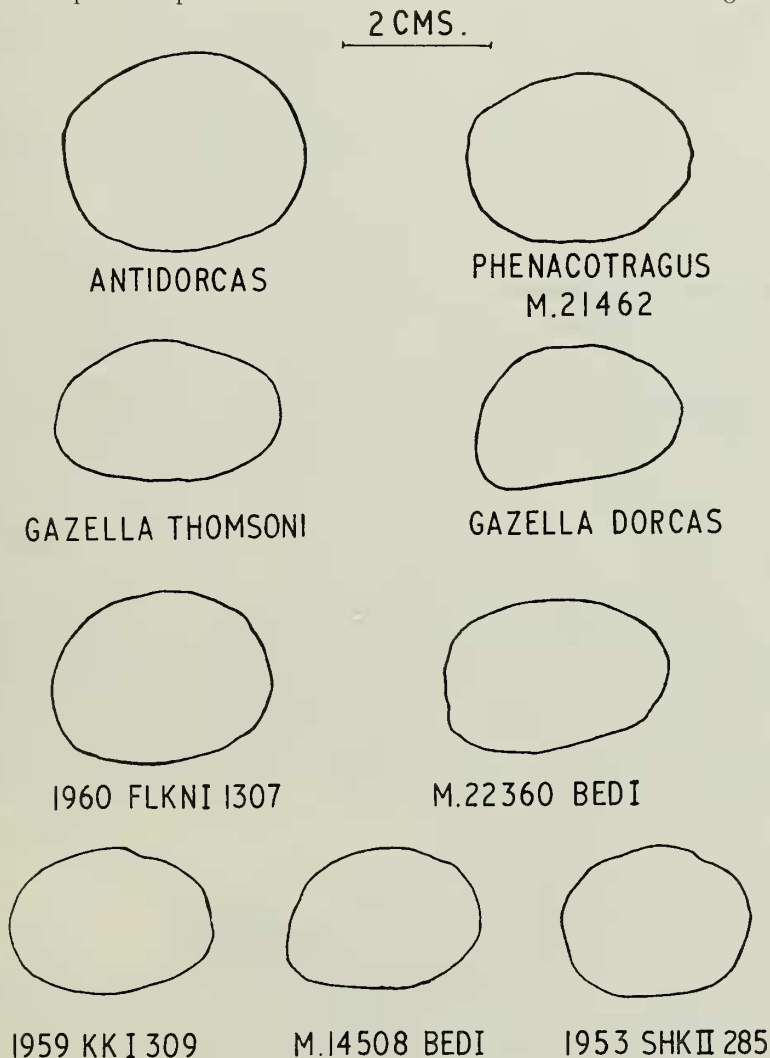


FIG. 7. Sections through gazelline horn cores.

The sections were taken at a distance above the pedicel equal to approximately half the antero-posterior diameter of the horn core in question. Thin wire was passed around the surface at right angles to the direction of the core, then carefully removed and its outline traced on paper. The lateral side of all the horn cores lies towards the bottom of the page, and the anterior side is on the right. The long axis of each section, here shown horizontally, is at a small angle to the mid-line of the skull.

Pleistocene are more like the Olduvai species, but they are larger, less sharply bent back and have more nearly triangular supraorbital pits.

The Olduvai species does appear to be conspecific with *Gazella wellsi* from South Africa. According to an unpublished paper by H. B. S. Cooke, this species possesses horn cores with pronounced transverse ringing which are sharply bent back near their base, little compressed, and without appreciable outward divergence in their upper parts. Its teeth are noteworthy for the shortness of their premolar rows and for hypsodonty. An undoubted female skull assigned to this species has the small horn cores characteristic of living gazelles, and is quite unlike the massive horn cores of the Olduvai skull 6334 which I believe to be of a female. Two factors may contribute to explaining this discrepancy. Firstly, the Olduvai female skull is likely to be from an older stratum than the South African one, which is from Bolt's Farm, a site belonging to the Swartkrans stage (see Cooke 1963 for a discussion of dating and correlation of African sites, and also for a record of South African sites from which *G. wellsi* is known). Secondly, the state of the female's horns may have varied among the populations of a wide ranging species. The extant Indian gazelle *G. bennetti* appeared to Ellerman & Morrison-Scott (1951) to be the eastern representative of *G. arabica* and they put both of them, along with other named groups, in the single species, *G. gazella*; yet the horns of the *G. bennetti* females in the British Museum (Natural History) are more reduced than in *G. arabica*. This difference between the females of *G. bennetti* and *G. arabica* is admittedly less than that between the skull 6334 and the Bolt's Farm female.

Beyond the genus *Gazella*, it is *Antidorcas* which most resembles this Olduvai gazelle. In the springbok the horn cores are sharply bent back, those of the females are sometimes less reduced than in living gazelles, the supraorbital pits are small, and the level of the frontals between the horn bases is higher than the orbital rims, the premolar row is short and P_2 is often lost. In his unpublished work on the South African *G. wellsi*, Cooke also has noticed springbok-like traits, but not sufficient of them to justify a change of the generic name. These similarities will be taken up later and considered in a wider context.

Other gazelline skull and teeth remains from Olduvai

- (A) Three horn cores 1959, KK I, 309 (Pl. 2C)
1959, HWK II, 472.

B.M. (N.H.) no. M.14512, Bed I, probably a surface find.

KK 309 and M.14512 are perhaps slightly smaller than *Gazella wellsi* while HWK 472 is smaller still and can reasonably be regarded as a female. All three are much compressed transversely and the cross section towards the tip shows a rounded anterior edge which narrows towards a fairly sharp posterior edge. The cross section in Text-fig. 7 is at a level comparable with the other sections but it is too low to show these features. The upper parts are sharply bent backwards but not appreciably outwards, and are like some horn cores of *Gazella wellsi*, e.g. 1960 FLKN I, 1307 (Pl. 1A), in this respect. They also have horizontal ridges on the lower parts of the anterior surface as in *G. wellsi*, but the shape of the cross section is different.

No gazelline fossils that I have seen from other sites are comparable to these horn cores, but it is impossible to say whether they are a separate species or a variety within *G. wellsii*.

- (B) Six horn cores 1953, SHK II, 285 (Pl. 2C)
 1955, BK II, 226
 1959, KK II, 224
 B.M. (N.H.) no. M.14507, Bed I, probably a surface find
 B.M. (N.H.) no. M.22362 from FLK II (Pl. 7A)
 1959, KK I, 310

They appear to belong to *Gazella*.

The first is the most complete and best preserved specimen. It is about equal to the size of a *G. thomsoni* male horn core and curves slightly backwards in its lower parts and slightly forwards nearer to its tip. The angle of insertion looks as if it is about equal to that of *G. thomsoni*. The lateral side is flattened, the medial side rounded and there is practically no transverse compression. The long axis of the cross section appears to be slightly less nearly parallel to the long axis of the skull than in *G. thomsoni* and the core diverges slightly more in anterior view. The pedicel

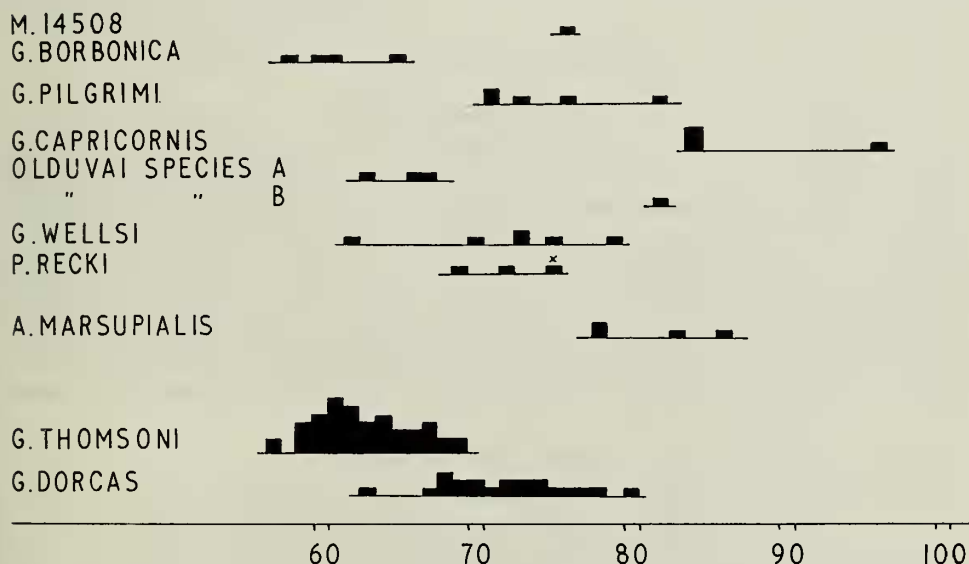


FIG. 8. Histogram of transverse diameter of horn pedicel as a percentage of longitudinal diameter. Only males have been measured in living species, but it is not certain that females have been excluded from among the fossils. The cross over one of the *Phenacotragus* readings marks M.21464, the supposed female. *G. capricornis* and *G. pilgrimi* are two Pontian species. *G. borbonica* is the Pleistocene species of Europe; all except one of the readings were taken on English specimens—the so-called *G. anglica*.

is rather short in front (not in BK 226 or M.14507), consequently the height of the otherwise large supraorbital pit is reduced. The level of the frontals between the horn bases is about the same as that of the orbital rims. BK 226, which is from the left side, has a slight anticlockwise torsion from below upwards. Two very much thinner horn cores may be the females of this species—M.22362 from FLK II and more doubtfully 1959 KK I 310.

Neither the horn cores of group (A) or (B) are like any living gazelle.

(C) Three lower jaws, 1957, SHK II, 793, (Pl. 3A).

1952, BK II, 152

1955, Bed II, MLK surface find

These lower jaws may belong with either of the two sorts of horn cores in group (A) and (B) above or with neither of them, although an association with (B) may be more likely because its horn cores are almost entirely of Bed II origin. SHK 793 is the best preserved, with all its adult teeth present except P_2 , which must have been destroyed after the animal's death. The length of the entire tooth row is about equal to that in *G. wellsi* but the premolar row is relatively longer. The length of the premolar row would have been about 2.3 cm. and the length of the molar row was 4.02 cm., thus the premolars' length was about 57% of that of the molars. The ramus is shallower below the teeth than in *G. wellsi* but the teeth do not look very brachyodont. It may have been not such a predominantly grazing gazelle as *G. wellsi*. The posterior half of the inner wall of P_4 is completely closed.

(D) One lower jaw—B.M. (N.H.) no. M.22379 (Pl. 3A).

This is an excellently preserved right mandible found in SHK, Bed II with the herd of *Phenacotragus recki* to be described later. It belonged to an adult, again about the size of *G. thomsoni*, and the teeth are not heavily worn. P_2 was present in life but has since dropped out. The posterior half of the inner wall of P_4 is completely closed. The depth of the ramus is as in the living *G. thomsoni*, and this separates it from the mandibles of group (C) and with less certainty from *G. wellsi*. The main point of interest is the long vertical ascending ramus; this and the morphology of the teeth separate it from the *Phenacotragus* herd with which it was found.⁵ The posterior half of the medial wall of P_4 is completely closed. It could be a later development from the *G. wellsi* stock of Bed I.

(E) Four lower jaws, 1960, FLKN I, 137, layers 1-2-3

1960, FLKN I, 1293, layer 1, (Pl. 3B)

1941, Bed I, F.109, surface find (Pl. 3B)

1941, Bed II, F.102, surface find,

together with some fragments of mandibles and isolated teeth.

There are several peculiarities in these lower jaws. The ascending ramus of 1293 rises high above the condyle for the squamosal articulation. Further, the horizontal ramus deepens rapidly as it passes back from beneath the premolars to the molars,

⁵ A larger non-gazelline mandible was also found with this herd, and is now in the British Museum (Natural History) although unregistered.

and although the 1960 pieces are from sub-adult animals, F.109 is adult and still shows the same character. The pattern of the occlusal surface of the molars is not like that usual for gazelles, instead it somewhat resembles that of *Aepyceros*, *Antilope*, and the teeth at the British Museum (Natural History) assigned to *Gazella mytilinii* (M.4181-85). The medial walls bulge outwards from the body of the tooth between the styles, the walls of the central cavities are more evenly curved and each cavity is wider at its ends than in the middle. M₂ of FLKN 137 has a goat fold and the P₄ of F.102 has an open anterior valley on its internal wall; F.102 also shows a trace of the root cavity for P₂. These finds are not unlike Arambourg's (1947) *Antidorcas* sp., although that form is larger according to the measurements given, and lacks P₂. It is quite possible that these animals were not gazelline at all.

(F) One horn core B.M. (N.H.) no. M.14508, Bed I, probably a surface find (Pl. 3C).

There are quite a number of unidentifiable, presumably gazelline horn cores from Olduvai, and this one is selected for mention because it is about the size of *G. thomsoni* and does not look unlike that species at first sight, with its flattened lateral surface and the supraorbital foramen lying in a moderately sized pit. However, the extent of the lateral compression is no greater than in *G. dorcas* or *G. rufifrons* among living species. M.14508 will be considered further in the discussion of the Kanam West horn core in Appendix II.

IV. GAZELLINE LIMB BONES

A large proportion of the gazelline fossils at Olduvai are of limb bones, and it is of obvious interest to compare them with living species. To this end Recent limb bones of some antelopes were first compared among themselves and the findings were given in Gentry (in preparation) in which it was found that gazelles are not easily distinguished from one another or from the springbok. However the situation with the springbok might have been remedied had more than three specimens of it been available. *Litocranius* (the gerenuk) and *Ammodorcas* (the dibatag) had several distinctive characters, and *Aepyceros* was the least difficult genus to distinguish from gazelles. Differences of proportion between the species and genera were not considered in that paper but are immediately below.

Proportions of limb bones

Measurements were taken of the length and least thicknesses of the limb bones of three *G. dorcas*, six *G. thomsoni*, ten *G. granti*, five *Aepyceros* and two *Antidorcas*. Histograms were drawn of the ratios of least thickness to length of each limb bone and of the length ratios metacarpal/humerus, radius/humerus, metatarsal/femur and tibia/femur. These histograms (Text-figs. 9, 10) are an indication of cursorial adaptation in the various species.

In gazelles, but not so clearly, or not at all, in *Aepyceros*, the females have more slender bones than the males and relatively longer distal bones. The ranges of combined male and female readings for ratios in the front legs are usually greater than

those in the hind legs. Among the three gazelle species it is *G. granti*, the largest one, which has the thickest bones and its distal bones relatively shorter than in the other two species. The small *G. dorcas* is at the opposite extreme as would be expected, and in its back legs the ratios of metatarsal/femur and tibia/femur are very different from *G. thomsoni* and *G. granti*. The femur and humerus of *G. thomsoni* and the femur of *G. dorcas* are relatively thicker than in *G. granti*.

So far as can be reliably judged from two measurable specimens, the springbok is characterized by very long and slender metatarsals, long radii and long metacarpals.

The impala differs from the other genera and species in its relatively long radius and short metacarpal and perhaps also in a slightly longer and thicker tibia. These characters are presumably adaptive to jumping.

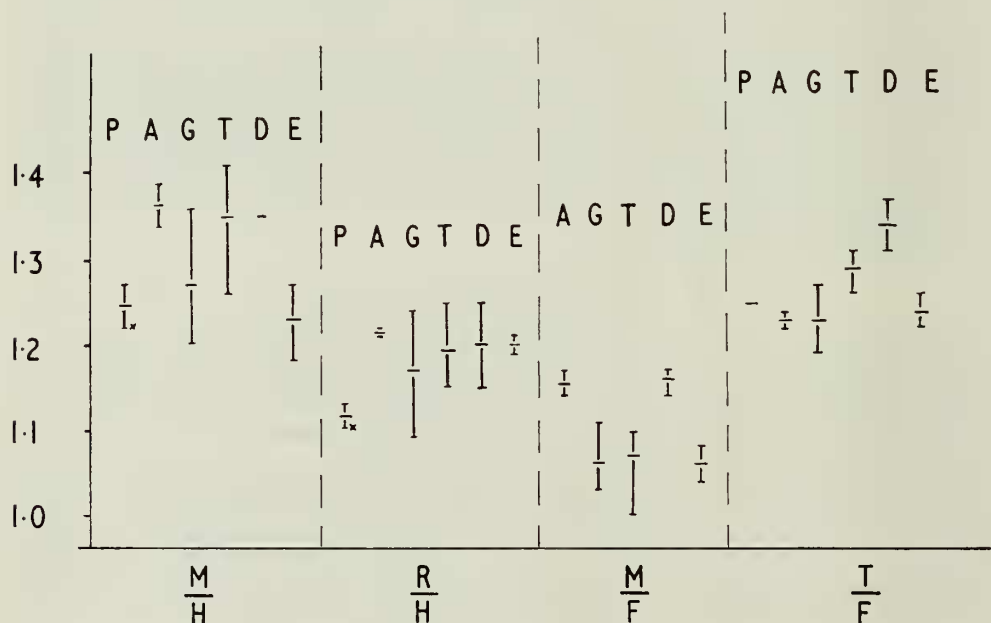


FIG. 9. Histogram of comparative lengths of limb bones.

$\frac{M}{H}$ = length of metacarpal/length of humerus; $\frac{R}{H}$ = length of radius/length of humerus;
 $\frac{M}{F}$ = length of metatarsal/length of femur; $\frac{T}{F}$ = length of tibia/length of femur;

P = *Phenacotragus recki*

A = *Antidorcas marsupialis*

G = *Gazella granti*

T = *Gazella thomsoni*

D = *Gazella dorcas*

E = *Aepyceros melampus*

W = 1960 fossils from Bed I.

The mean value and observed range are shown for each ratio in each species. Within *G. granti* and *G. thomsoni* the females have longer distal bones and thinner bones than the males, although this is not shown on the histograms. Crosses mark the fully adult individual of *Phenacotragus*.

*Limb bones of fossil gazelline species from Olduvai**Femur*

Only a few fragmentary remains of femora are available from the 1960 dig. FLKN I, layer 1, 1027 (Pl. 4A), is a proximal end with the top of the great trochanter missing. Its chief point of interest is a short, not very high, but sharp, vertical ridge on the anterior surface just below the lateral end of the articular head. In this position it forms the lateral boundary of the vastus medialis and intermedius origins. The ridge is only present in such a pronounced form in one of the eighteen femora of living gazelles available for comparison although there was a tendency towards it in some *G. granti*; it was also seen in a male springbok femur at the University Museum in Oxford in which it was less sharp, but in no other genus. The neck supporting the articular head of the fossil can be seen in medial view to be as thin as in living species. The gluteus accessorius insertion lies forwards. The hollow between the great trochanter and the articular head is not so deep in anterior view as in living species. The size of the fossil is of an animal intermediate between *G. granti* and *G. thomsoni*. FLK I, K, upper levels is a left proximal end with the hollow between the articular head and the great trochanter rather shallow and the medial part of the articular head projecting somewhat forwards from its neck,

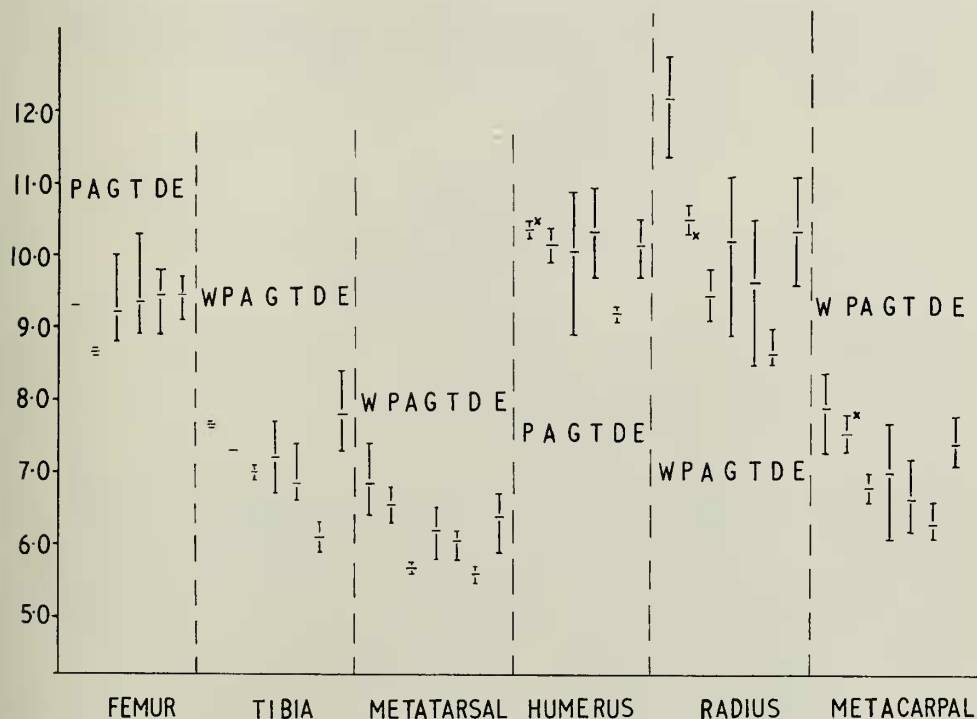


FIG. 10. Histogram of least thicknesses of limb bones. Initials as in Text-fig. 9.

thereby showing a puzzling resemblance to reedbucks in one character and to sheep and goats in the other. FLKN I, layer 1-2-3, 28 is a shaft with distal end. If one looks at it in ventral view, the part behind the origin of the lateral femoro-tibial ligament looks slightly more convex than in living gazelles. This difference is slight, and otherwise the fossil bone and Recent bones are indistinguishable. The top of the lateral condyle is flat as in *G. thomsoni*, and the size is about that of *G. thomsoni*. FLK I, F/15, 150 is a similar distal end.

A number of other articular heads are quite likely to be gazelline, among them FLKN I 402 and FLKN I 6242.

Tibia

There are more tibiae than femora from the 1960 Olduvai excavations:

complete bones	FLK I, F.161 (Pl. 4B) FLKN I, layer 1, 1246 and 1284 (probably the same individual)
almost complete	FLKN I, layer 2-3, 685 FLKN I, layer 1-2-3, 157
proximal ends	FLKN I, layer 2-3, 658 FLKN I, layer 1-2-3, 492 (only the back part of the articular surfaces)
distal ends	FLK I, 257 FLK I, 510 ⁶ FLK I, 664 FLKN I, layer 1, 1564 ,, 2-3, 651 FLKN I, layer 3, 1157, 6087, 6183, 6270, 6290 ,, 5, 1818, 5189 ,, 1-2-3, 81, 931

The tibiae seem to belong to an animal about the size of *G. thomsoni*; the top articular surface is about the size of that species but the length is less. The thickness of some of them is greater than in *G. thomsoni*; of others about the same. The only two measurable ones are so thick as to be outside the range of *G. thomsoni* (see Text-fig. 10). No good difference is discernible between the FLK and the FLKN remains, but both show some differences from living gazelles. Towards the proximal end, the posterior surface is less flattened and more convex and the subsequent raising of the ridges for the long digital flexor origin gives the bone an appearance reminiscent of Reduncini. The long digital flexor ridge lies more closely to the medial edge of the posterior side than in living gazelles; a condition almost like that of the impala, *Aepyceros*. The lateral surface of the cnemial crest is noticeably concave, perhaps more than in *G. thomsoni*. The long axis is curved

⁶ This is from level G.15, together with another unnumbered distal end. Three more unnumbered distal ends are from FLK I level G.13; all other FLK I fossils throughout this paper are from the Zinj level.

forward at the top and bottom of the bone more than in any living gazelline species. It seems very unlikely that distortion could be responsible for this in so many specimens. At the distal end the medial malleolus is shorter and its posterior wall more diagonal than in living species. Also at the distal end the level of the anterior top edge of the fibula bone looks as if it is less high than in living species, but this is not a certain difference, and it is too easy to anticipate it from the character of the medial malleolus on the opposite side. In other characters the fossils agree with living gazelles.

M.14618 is a proximal end from Bed I, and is apparently identical with the above remains. It shares with FLK I, F.161 a greater slope of the surface for the insertion of the ligament from the patella at the top of the cnemial crest than in the only complete top end from FLKN I—number 1284. But this is probably not beyond the range of intraspecific variation. 1957, LK I (surface find) 891 also agrees with the distal ends. Alcelaphine distal ends are almost indistinguishable from those of gazelline genera, and there are a number of indeterminate specimens (e.g. M.22349-53). The absence of comparably large gazelline-like limb bones other than tibiae decreases the likelihood of these ones belonging to the Antilopini.

Metatarsal

A number of fairly complete metatarsals are available from the 1960 dig :

complete	FLK I, C.1227, F.219
	FLKN I, layer 1-2-3, 3, 199, 464, 530
	„ 3, 6198
Proximal ends	„ 5, 1454, 1758, 5194
	FLK I, C.1054, G.358
	FLKN I, layer 1-2-3, 527
distal ends	„ 2-3, 671
	FLK I, D.124 + D.26 (two pieces of the same bone)
	FLKN I, layer 3, 6184
	„ 2-3, 740
	? , 758
	layer 1-2-3, no number
	„ 1, no number.

They are shorter than in *G. thomsoni* but thicker ; the distal end FLKN I 740 has the least transverse thickness. Those from FLK are slightly larger than those from FLKN. They differ from living species in that the naviculo-cuboid facet is slightly larger in comparison with the facet for the ectocuneiform. The naviculo-cuboid facet is not actually larger than the ectocuneiform facet, only less reduced than in living species. This can be seen in the histogram on Text-fig. 11. The difference between these fossils and *G. granti* for linear measurements across the two facets was 5.5 ± 4.73 with 16 degrees of freedom, a small difference with wide confidence limits. However it probably is a true difference and it is likely that there is a tendency to reduce the area of the naviculo-cuboid facet in gazelline evolution.

An alternative measurement from the front to the outermost point of the rear edge of the naviculo-cuboid facet, instead of to its central point, when compared with the readings for the ectocuneiform facet gave a non-significant difference from *G. granti*. The front of the top articular surface is less upcurved than in living species. There are no other sure differences from living gazelles.

FLKN I, layer 1-2-3, 613 is a distal end from the 1960 excavations which is too large to belong to the above species. It is about the size of a small *G. granti* and is definitely gazelline by the prominent anterior flanges above the condyles. FLKN I, layer 3, 5000 is a complete metatarsal which could conceivably belong with 613 or with most of the metatarsals considered above. However it is difficult to visualize such a slender bone as 740 in the same species, so 5000 may provisionally be placed with 613. As far as size is concerned the proximal femoral end FLKN I 1027 would go with these two metatarsals. There is no other reason why the femur and metatarsals should be put together, but it is instructive to find out the minimum number of species to which the fossil limb bones may be assigned.

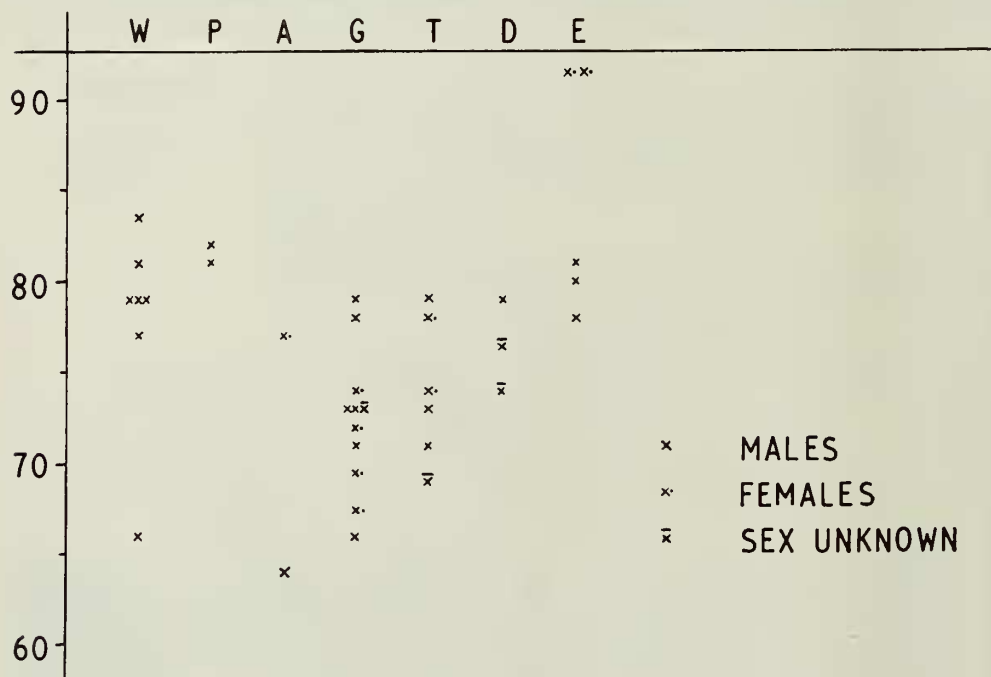


FIG. 11. Histogram of length of the metatarsal's naviculo-cuboid facet/length of its ectocuneiform facet. $\times 100$. The measurement of the naviculo-cuboid facet was taken from its most anterior point at the junction with the ectocuneiform facet to the centre of its rear edge. The measurement of the ectocuneiform facet was from the anterior point of the junction with the naviculo-cuboid facet to the point where its rear and medial edges meet. The initials are as on Fig. 9. *Aepyceros* probably has a relatively larger naviculo-cuboid facet than in gazelles, as the 1960 fossils from Bed I might also have done.

A proximal end 1959, KK I, 248 is about the same size as the majority of the 1960 bones but shows a number of clear cut morphological differences. The posterior hollow at the top is shallow and without a foramen; there is a small hump on the edge of the posterior side lateral to where the foramen would have been if it were present. The groove down the anterior surface is better shown than in other fossils and there is a ridge medial to the lateral extensor tendon at the top of the anterior surface. This proximal end could easily be from the same individual as a distal metatarsal end KK 249 which has the gazelline prominent flanges above the distal condyles. If KK 248 is gazelline it is from a peculiar species, if it is not gazelline its affinities are very obscure. The combination of shallow posterior hollow, anterior groove and the ridge at the top of the anterior surface is also found in the Caprinae.

Astragalus

FLKN I, layer 1-2-3, 10, 577

„ 2-3, 708

„ (?), 1564

and two from FLKN I without numbers.

They are about the size of *G. thomsoni* and differ from those of living gazelles only in that the lower part of the lateral side is more deeply excavated. FLKN I, trial trench, layers 1-2-3, no number, is about the size of a springbok astragalus and thus perhaps too large to belong to the above species. It differs further in having a less deeply excavated lower lateral side.

Naviculo-cuboid

FLKN I, layer 1-2-3, 15, 81, 924 (and one without a number, from layer 3)

They are about the same size as in *G. thomsoni* and differ from living species of gazelles only in having the posterior wall project less when it is seen in medial view. 1959, HWK II, 5 could belong to this group. FLKN I, 1564 has its posterior wall projecting so little that it may be a separate species from the other four above.

Scapula

FLK I, D.177

FLKN I, layer 3, 1358, 1359, 1740, 6076

FLKN I, layer 1-2-3, 820

Only the stems have been preserved in 1740 and 6076. They do not differ from the scapulae of living gazelles except perhaps in a less concave surface for the origin of the teres minor and long head of the triceps. 1959, KK I, 478 probably also belongs here. An unnumbered stem from FLKN I and a stem FLKN I, layer 1, 1467 are separable from the others by being larger and having flatter medial sides. They may be of a different species.

Humerus

Proximal ends	FLKN I, trial trench, layer 3, fall FLKN I, layer 1, 1307, and one without a number
Shaft	FLKN I, layer 1, 1593
distal ends	FLK I, C.1181 (fits radius C.1176 and olecranon C.1177) FLK I, B.135 (fits radius B.136) FLKN I, layer 1, 1346 FLKN I, layer 1, 1418, 1730 FLKN I, layer 1-2-3, 54, 71, 381, 587, 633, 654
	FLKN I, layer 3, 6092 FLKN I, layer 1-2-3, 9031 FLKN I, layer 5, 1207, 1813 FLKN I, one with no number from layer 1

No complete gazelline humerus was excavated in 1960. The most nearly complete specimen with a proximal end present is labelled FLKN I, trial trench, layer 3, fall. It would probably have been slightly shorter than in the living *G. thomsoni* but no less thick. Although the medial tuberosity is missing, the top of the bicipital groove may be at a lower level relative to the front of the articular head than is usual in living gazelles. In its other characters this humerus is just like that of a living gazelle. The two other fragmentary proximal ends and the shaft cannot be separated from the above piece.

There are a large number of distal ends of humeri ranging in size from being intermediate between *G. granti* and *G. thomsoni* (e.g. FLK I, C.1181) down to the size of a rather small *G. thomsoni* (e.g. FLKN I, 1730). Apart from the size range there are also morphological differences. Thus FLKN I, layer 1, no number and FLKN I, 1207 have relatively less high medial condyles, and three other distal ends (FLKN I, 1813, 6092, and 9031) have the top of the articular facet extending less far into the coronoid fossa on the anterior surface which has the effect of lowering the height of the medial condyle. But in the rest of the 1960 fossils, as well as in living gazelles, the humerus has a relatively high medial condyle and the top of the articular facet extends far into the coronoid fossa. It is reasonably certain that more than one species is present among the 1960 humeri but classifying the intermediates is impossible.

Radius

Complete	FLK I, D.100 FLKN I, layer 1-2-3, 70, 50 (same individual as 70?) FLKN I, layer 2-3, 666, 682, 730, and one without a number from layer 5
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proximal ends	FLK I, B.136 (fits humerus B.135)
	FLK I, C.1176 + C.1177 (fits humerus C.1181)
	FLKN I, layer 1, 1480
	layer 3, 6809
	layer 1-2-3, 269 and one with no number
	layer 5, 1448 and 1816
distal ends	FLKN I, layer 3, 6105

The 1960 radii are about the same length as in *G. thomsoni* or slightly less but they are more massive than in any living gazelle, as can be seen in Pl. 4C. They differ from living gazelles as follows. The antero-medial corner of the medial facet on the top surface has as sharp an angle as in *G. thomsoni* and *G. rufifrons*; such a corner occurs also in *Aepyceros*, *Litocranius*, *Ammodorcas*, and *Antidorcas* but is not well seen in other living *Gazella* species. In some of the fossils the side edge of the medial facet is also angled, and this can be clearly seen only in *G. thomsoni* among living species. The medial facet is but little indented along its posterior edge; this is like *G. thomsoni*, *G. dorcas* and *Aepyceros* among living forms, whereas *G. granti*, *G. spekei*, *Antidorcas*, *Ammodorcas* and *Litocranius* are indented. The lateral facet is as flattened as in two of the three *Antidorcas* skeletons and *Aepyceros*, but it is not so long as in *Aepyceros*. The tubercle for the lateral humero-radial ligament projects less far and is slightly lower on the shaft than in living gazelles. There is perhaps less torsion of the stem, but this is rather uncertain. At the distal end the medial edge of the scaphoid facet projects further ventrally than in living gazelles; in this it is perhaps like the impala and the springbok. Apart from the 1960 radii, the proximal ends 1959 KK I 289, 1959 MK I 36 and 1959 HWK II 417 and the distal ends 1959 KK I 262, 1959 HWK II 416 and 1953 BK II Extension 42 may best be put in this group.

Four radii excavated in 1960—FLKN I, layer 1, 1010, 1300⁷, 1605 and FLKN I, layer 3, 6049—are smaller than the group described above and have medial facets which are more compressed antero-posteriorly. These radii could be put with the humeri with rather low distal medial condyles since one would expect low humeral condyles to go with short medial facets on the radii. From the point of view of minimum number of species the naviculo-cuboid FLKN I 1564 could join these fore-limb bones.

Metacarpal

Complete bones	FLK I, D.133
	FLKN I, layer 1, 1273, 1306
	layer 3, 6050
	layer 2-3, 762, 764
	layer 5, 1450

⁷ Probably the same individual as 1010.

Proximal ends	FLK I, D.33-36
	FLKN I, layer 1, 1276, 1481
	layer 3, 5161 + 5164, 6100, 6194, 6255
	layer 1-2-3, 840
Distal ends	FLKN I, 1482

Most of the metacarpals are shorter than those of *G. thomsoni* but more massively built. The complete one from FLK is slightly larger than those from FLKN I. They differ from living gazelles in the following characters. There is a better developed anterior proximal foramen, some of them have the posterior edge of the top articular surface indented, or not so completely continuous as in living species, an angled antero-medial corner of the magnum-trapezoid facet is poorly present as in *Gazella* except *G. granti*, and the angled corner on the antero-lateral side of the unciform facet is intermediate between its condition in *Litocranius* and in the living species of *Gazella*. The fossils agree with living gazelles in the lack of a concavity down the posterior side of the shaft.

The five pieces FLK I D.33-36, FLKN I 1481, 6050, 6100, and 6255 could be separated from the rest of those in the above list on the grounds that the posterior indentation of the top articular surface and the angled corner on the unciform facet are better developed. If this separation should be valid, the most likely assignment of these metacarpals would be with the humeri with small medial condyles and radii with antero-posteriorly compressed medial facets. But on the present evidence such a separation is doubtful.

FLKN I, layer 2-3, 655 is a complete metacarpal which differs from the bones above (but is probably not a separate species) in having a sharper corner of the antero-medial edge of the magnum-trapezoid facet, in being slightly more hollowed towards the top of the posterior side, in the shaft being more transversely compressed, in having large shallow hollows above the distal condyles on the posterior side and in the spaces for the tops of the phalanges above the condyles anteriorly being more restricted.

The distal ends FLK I D.120 and FLKN I, layer 1, 966 are larger than any of the previously mentioned metacarpals. They might be a separate species. The flanges of the condyles project less strongly from the medial facets of the condyles than in the above groups. The distal end FLKN I 1443 has hardly larger dimensions than the first group but may be placed with D.120 and 996.

Conclusions

The question arises of whether to allocate the main mass of the fossil limb bones to *G. wellsi* or not. There is no definitely proved association with the skull parts and only the radii, metacarpals and, more doubtfully, the naviculo-cuboids are distinguishable from those of *Phenacotragus recki* to be described next. While it is probable that the most numerous gazelline limb bones at a site go with the most numerous remains of skulls and teeth, the more prudent course is to say that the limb bones probably are those of *G. wellsi* with which they agree in size, despite a

few Bed I remains which appear to be *Phenacotragus*. They have a surprising number of differences from living gazelles. These differences and their massive proportions are extra evidence for the view that the gazelline fauna of Olduvai Bed I is markedly different from that now existing in Africa. The limb bones will henceforth be referred to as the 1960 fossils.

Several of the larger bones may tentatively be put together; these are the scapula 1467 from layer 1 of FLKN I and the unnumbered companion piece, the femur 1027 from layer 1, the metatarsals 613 from layer 1-2-3 and 5000 from layer 3, the metacarpals 996 from layer 1, 1443 from layer 5, 120 from site FLK I, and an unnumbered astragalus. They may be from a separate larger gazelline species, or they may be evidence of size changes within *G. wellsi* or *Phenacotragus*.

The table below relates the fossil remains of skulls and teeth to those of limb bones as far as is possible.

	Horn Cores	Jaws and Teeth	Limb Bones	Main Occurrences
I. <i>Phenacotragus recki</i>		As listed later		Bed II and probably also I.
II. <i>Gazella wellsi</i>		As previously listed		Bed I, probably later also.
III. Larger gazelline species	none	maxilla 1662?	femur 1027 etc., as in last paragraph.	Bed I.
IV. Gazelline species	group (A)	mandibles (C) or (D). Mainly upper part of Bed II	humeri with low medial condyles, radii with short medial facets, metatarsals KK I, 248 and 249.	Bed I and lower part of II for horn cores.
V. <i>Gazella</i> species	group (B)	mandibles (C) or (D). Mainly upper part of Bed II.	as for IV above?	Upper Bed II for horn cores.
VI. <i>Gazella</i> species	M.14508	mandibles (E)	as for IV above?	Beds I and II for mandibles.

Site HWK II is in the lower part of Bed II;
sites BK II and SHK II in the upper part.

It would be surprising if the mandibles (E) were in fact conspecific with the horn core M.14508, but the table gives a minimum number of species. The question of how many species occurred together at any one time in the Olduvai region will be answered as stratigraphical details become more precisely known.

V. NEW MATERIAL OF *PHENACOTRAGUS*

Phenacotragus recki (Schwarz)

(Pls. 5-8)

1932 *Adenota recki* Schwarz : 1, text-figs. 1, 2.

1937 *Phenacotragus recki* (Schwarz) Schwarz : 53, pl. 1, fig. 1.

Schwarz (1937) described this species more fully than in 1932 mainly on a skull excavated from Olduvai Gorge in 1913; its stratigraphical provenance within the

gorge is unknown. A cast of the type skull is in the Department of Palaeontology, British Museum (Natural History), no. M.21460. Most of the new material described here belongs to an excellently preserved herd excavated from site SHK II in 1935. According to Dr. L. S. B. Leakey the herd was discovered in clays about 300 feet from a living floor near the base of the upper part of Bed II. It is likely that the herd was entombed in a muddy swamp (into which it had perhaps been driven by the men inhabiting the living floor?). The minimum number of individuals in the herd, based on the metatarsals, is nine or ten, all but two of which are juvenile or young animals.

MATERIAL. The list of skull parts comprises the following :

M.21462	adult frontlet (Pl. 5)
M.21464	cranium and upper teeth of a young adult (Pls. 5, 7C)
M.22436	two mandibles with complete adult dentition (probably the same individual) (Pl. 8A)
M.22378	adult mandible
M.22371	adult basioccipital (Pl. 7B)
M.22372-77	maxillary and mandibular pieces, mostly sub-adult
M.22380-83	

The following pieces from the 1960 dig are also assigned to *P. recki* :

1960, FLKN I, layer 1-2-3, 627	maxilla and upper teeth
„ „ trial trench, 6176	fragment of juvenile maxilla
„ „ layer 1, 1281, 1327, 1511	fragments of juvenile maxillae
„ „ layer 3, 6044	fragment of right mandible
„ FLK I, B.119	fragment of right mandible
„ FLKN I, layer 5	right horn core (Pl. 7A)

The following three horn cores, from years other than 1935 or 1960 are also included :

1955, BK II, 71
B.M. (N.H.), M.14513, Bed I, probably a surface find (Pl. 7A)
B.M. (N.H.), M.15862, Kanjera, Kenya. (Previously identified as this species by Dr. A. T. Hopwood.)

The frontlet M.21462 (Pl. 5) has horn cores which are oval in cross section without any flattening of the lateral side or tendency to form a postero-lateral edge. Horizontal ridges can be seen on the lower antero-lateral parts of the horn cores. They are not very steeply inserted on the frontals, their basal portions rise parallel to one another then bend backwards and outwards, and taper gradually to a point. The supraorbital pits are small and the level of the frontals between the bases of the horn cores is higher than the orbital rims. The left orbital rim is complete in its dorsal part and is rather wide compared with the width apart of the pedicels of the horn cores.

The horn cores on the cranium M.21464 (Pl. 5) are shorter and their distal parts are not so strongly bent backwards as in M.21462. From the appearance of the surface of the horn cores it can be inferred that M.21464 is a younger individual than

M.21462, but while further growth could have caused the distal parts to bend back as strongly as in M.21462, their tapering towards the tip would not have been drawn out over such a long distance. The *Phenacotragus* horn cores can be distinguished from those of *Gazella wellsi* by being more nearly parallel at the base in anterior view and then more outwardly divergent in their distal parts. They are also more symmetrical in cross section and lack the flattened lateral surface of *G. wellsi*.

The orbital rims are again wide in M.21464, and the braincase is very narrow. The braincase looks as if it is shorter than in a gazelle and its top surface is less flat in profile than in males of *G. thomsoni* or even *G. rufifrons*. Preorbital fossae are present and are about as extensive and deep as in a female *G. thomsoni*. The basioccipital is like that of a young *G. thomsoni* or a *G. dorcas*; no very profound conclusions can be drawn from this since the basioccipitals of all young gazelles look similar to *G. dorcas* and it is not surprising that one in a related genus does also.

A separate basioccipital, M.22371 (Pl. 7B) is from an adult skull, possibly M.21462, and this is quite unlike most living gazelline forms. The anterior tuberosities are close together and the longitudinal ridges are almost non-existent. The nearest approach to this sort of basioccipital is found in some individuals of *G. bennetti* of India, and an almost identical one is seen in the type cast skull of *P. recki* in the British Museum (Natural History). An isolated nasal bone has survived; it is not complete anteriorly, but even in this state it is longer than in any living gazelle.

At a fairly late stage of the work it was noticed that if only an isolated horn core of M.21464 had survived instead of the whole cranium it would have been very much like the four horn cores at the end of the list—1960 FLKN I (?),⁸ 1955 BK II 71, M.14513 and M.15862. The last one, from Kanjera, had in fact already been labelled as *Phenacotragus recki* by Dr. A. T. Hopwood (see Kent 1942). But if these four horn cores are of the same species as M.21464, and if M.21464 and M.21462 were of the same species as the cast of the type skull—M.21460—the problem arises of allocating the horns and skulls to the different sexes. The four horn cores at the end of the list are so much smaller than M.21460 that they must be the females and M.21460 the male. None of the last four shows any signs of being from young animals, nor is it conceivable that they could grow into the shape of M.21460. These presumed female horns differ from the male by being less backwardly bent, probably less outwardly divergent in their distal portions and, in M.14513, in tapering to a point over a much shorter distance. As in the Olduvai *Gazella wellsi* they are more bulky than in the females of living gazelles. Females of other gazelline genera except *Antidorcas* are hornless.

While M.21464 may be accepted as a female on the assumption that its horn cores have almost stopped growing, it is difficult to place M.21462. It is an adult animal, and if a female its horns are unexpectedly large. On the other hand they are smaller than in M.21460. It would be a great help if the horizon of M.21460 were known, for over such a long period of time as is represented at Olduvai changes in body size of the species or immigrations of different *Phenacotragus* species are quite possible. The probability is that M.21462 is male.

⁸ The number has become illegible, but the horn core is from layer 5.

It is interesting to note in the supposed female horn cores of *P. recki*, that while the basal parts are bulky for their size, the distal parts are either short as in M.14513, or if they are long then the whole length of the distal parts has a much reduced girth compared with the basal parts as in the horn core from 1960 FLKN I, layer 5 (and to some extent in M.21462). Such a pronounced reduction in girth of the distal parts is not known in the horns of female living gazelles. In these, the female horn cores are uniformly thinner than those of males down their entire length; as may also be seen in the two horn cores assigned to the *Gazella* species of group (B) at Olduvai (Pl. 7A).

Upper teeth

The upper teeth of *P. recki* are undoubtedly gazelline but the molars differ from living gazelles and from the Bed I teeth supposedly belonging to *G. wellsi* in the more prominent mesostyle on the outer wall and in the tendency towards a concave outer wall of the posterior part of the tooth. In M.21464 (Pl. 7C) the junction of anterior and posterior parts of the molars is wider than in gazelles at the same stage of wear owing to the less deep incision of the inside wall. The M³s of M.21464 have not completely erupted, and they show the hypsodonty of *P. recki*. The length from the neck to the occlusional surface down the outside edge between the anterior and posterior lobes is 3.00 cm., while the length of the base of the erupted part along the jaw line is 1.32 cm. The length of the adult premolar row can be measured on FLKN I 627, and on the type skull, and can be approximately estimated for M.21464 in which P² is missing. It is clear from Text-fig. 6 and from previously given values that the premolar row is probably shorter than in living gazelles and may be as short as in *G. wellsi*.

Some teeth from the 1960 dig in FLKN I, upper molars 121 and 122, two unnumbered upper molars and a piece with P³ + P⁴, are larger than the other teeth from that site and have the morphology of a *Phenacotragus*. On Text-fig. 5 the length of 122 has been plotted on the assumption that it is an M², and it falls well within the possible size range of the Bed II species. However it is true that 122 is only very slightly smaller than the M² of the upper dentition FLKN I, 1662, already mentioned in the account of *G. wellsi*, and the size of 1662 is matched by fragments of lower jaws from Laetolil (1959, nos. 150, 151, 294 and 443 + 444—see Appendix II) which look as if they belong to a larger species of *Phenacotragus* than is represented by the SHK II herd. The previously mentioned large gazelline limb bones from Bed I (scapula FLKN I, 1467, femur FLKN I, 1027 and others) could go with these teeth remains. So there is evidence of at least one larger sized gazelline species in Bed I and at Laetolil, but it cannot be definitely regarded as closer to *Phenacotragus* than to *Gazella wellsi*.

Mandibles

The lower molars are distinguishable from gazelles by having medial walls of the anterior and posterior lobes which are less curved outwards from the body of the tooth in question, and by having still less of a tendency towards the development of

goat folds. In addition the posterior deepening of the horizontal ramus (Pl. 8A), involving a change in direction of its lower edge at about the level of M_2 , is more pronounced than in gazelles, and the ascending ramus of the left side of M.22436 is less tall than in gazelles. The tooth differences alone are not so surely perceptible in older individuals, and unless the mandible itself is also well preserved the generic separation may not be certain.

While the separation of the mandibles from those of *G. wellsi* in Bed I may seem well established at first sight, it must be noted that only the left M.22436 among the *P. recki* mandibles is both adult and complete, and that only FLK I, G.323 from *G. wellsi* is really adequate for comparison with any other species. Also the juvenile bones of both species are similar—M.22372 of *P. recki* has an ascending ramus shaped more like that of *G. wellsi* than have adults of its own species, and a number of juvenile mandibles in Bed I (FLKN I, layer 1-2-3, 231; layer 1, 1310; layer 5, no number; FLK I, 8 and 188) are like *Phenacotragus* in their tooth morphology and in the shape of the horizontal ramus anteriorly. But if the juvenile mandibles from Bed I are referred to *P. recki* then the older mandibles alone are left as *G. wellsi* which is clearly an unsatisfactory situation. None the less, by observing the characters of shape and height of the ascending ramus, depth of horizontal ramus and course of its lower edge, and the morphology of little-worn adult molars, a distinction should be possible with adequate samples.

Concerning the premolars, the posterior part of the inner wall of P_4 is closed in M.22436 and P_2 is very much reduced, but in M.22378 the posterior part of the inner wall of P_4 is open and the socket of P_2 suggests that it was larger than in M.22436.

The principal reasons for assigning this herd of gazelline antelopes to *Phenacotragus recki* lie in the resemblance of the horn cores and frontals region of M.21462 and M.21464 to the cast of the type skull (Pl. 6), the resemblance of the upper teeth morphology and proportions, the similarity of the basioccipitals and the long nasal bone found with the 1935 herd.

The differences of the type cast from the frontlet and cranium M.21462 and M.21464 are only minor. The type skull is larger, and its longest molar, M^2 , is only barely shorter than the upper molar FLKN I, 122 which was considered perhaps too large to belong to the same species as the SHK II herd. Also the basal part of the type skull's only surviving horn core is longer before bending backwards and a little more divergent in anterior view. The course of its upper parts is rather more of a spiralization than a simple backwards and outwards bend. No transverse ridges occur towards the base. The basioccipital is longer with a deeper valley between the anterior tuberosities, the descending flanges of the basisphenoid originate more anteriorly, the upper molars have more sharply pointed inner lobes and lack marked concavities of the posterior halves of their lateral walls, and the preorbital fossa is a little smaller. The first four differences (size, longer basal part of the horn core, more divergent, spiralization) could be due merely to age or sex factors, while the presence or absence of transverse ridges on horn cores is a variable character within other gazelline species. The last five differences are insufficient to place the 1935 herd beyond a legitimate range of variation from the already named type skull,

especially when the unknown horizon of the type is remembered. However, since the horizon of the type is unknown, since the above differences might not be due to age or sex, and since there is evidence of a larger gazelline species which might well be conspecific with the name-bearing type of *Phenacotragus recki*, then it is still possible that further finds will show that the 1935 herd should be placed in another and smaller sized species of *Phenacotragus*. At present one could not write two clearly distinct diagnoses with any firm basis, and the fossils may be from one lineage which varied in size at different periods.

The limb bones of PHENACOTRAGUS RECKI (Pl. 8B, C)

Schwarz (1937) thought that within the Antilopini, *Phenacotragus* was related to *Aepyceros*, the impala. This question will be discussed later, and in the following account of limb bones *P. recki* will be compared both with the impala and with living gazelles.

Pelvic girdle

Among the bones of the herd excavated from SHK II in 1935 are two sides of a sub-adult pelvic girdle (M.22451), two juvenile left sides (both numbered M.22391) and a juvenile right side (M.22392). The minimum number of individuals represented is three. The sub-adult girdle is smaller than in *G. thomsoni*. It differs from living gazelles only in that the articular facets at the back of the acetabulum are not so close to one another, but this difference might disappear in older individuals.

P. recki is unlike the impala in not having a low rear part of the pubic symphysis, in its well marked medial origin for the rectus femoris muscle, and probably also in the origin for the iliacus extending backwards along the lowest part of the lateral side of the ilium. The outline of the top part of the front edge of the ilium cannot be seen in *P. recki*.

Femur

There are two sub-adult femora in which the epiphyses have started to close (M.22452-53), four juvenile femora (three numbered M.22422 and one M.25038), and a juvenile distal and proximal end (M.22423 and M.22393). The minimum number of individuals in the herd based on femora is four.

The two sub-adult bones, almost certainly from the same individual, differ from living gazelles in the following respects: the stem supporting the articular head is more massive in medial view of the proximal end. The effect of this, in conjunction with the deeper rear edge of the acetabulum of the pelvis, would be to restrict the backwards stride of the femur compared with modern gazelles. But this character may not have persisted in older animals; in *G. thomsoni* it is more marked in young animals. Secondly the medial end of the proximal articular head lies relatively more posteriorly in the fossil. This may best be seen by laying the bone on a horizontal surface with the anterior side upwards. The articular head of the fossil is then in more or less a horizontal plane while that of a living species is directed more diagonally. The effect of this would be that the distal end of the

femur in a living species swings further outwards as it is protracted than in *P. recki*. Thirdly at the distal end of the femur, the side of the lateral condyle looks more convex behind the pit for the femoro-tibial ligament; this is best seen in ventral view. Lastly, the hollow for the ligamentum teres on the articular head is deeper.

P. recki is unlike the impala in the position of the gluteus accessorius insertion and the absence of a separate crest above the accessorius for the rear parts of the vastus lateralis. The convexity of the distal lateral condyle and the deep hollow on the articular head are, however, nearer to the condition of the impala than gazelles are. Older individuals of *Phenacotragus* would be needed to see which genus it resembled in the outline of the top of the great trochanter.

Tibia

There are two sub-adult tibiae in which the sutures are closing (M.22454-55); they are almost certainly from the same individual and moreover from the same animal which supplied the sub-adult femora (M.22452-53). In addition there is an adult distal end of a shaft (M.22394) and eight juvenile tibiae (M.22395, M.22424, three of M.22425, two of M.22426 and M.22427). The minimum number of individuals is seven.

They are hardly distinguishable from gazelles except in the following respects. The long axis is curved forwards at the top and bottom to an extent which is intermediate between living gazelles and the 1960 fossil tibiae from FLK and FLKN. Distally the medial malleolus is neither so curved nor so long as in living gazelles. Despite being rather smaller than *G. thomsoni*, the sub-adult tibia falls above the average values of *G. granti* and *G. thomsoni* for thickness and almost on the mean value of *G. granti* for length compared with that of the femur (Text-figs. 9, 10).

The *Phenacotragus* tibiae differ from the 1960 fossils in having a less convex posterior surface towards the top and in the longitudinal digital flexor ridge being closer to the lateral side. The cnemial crest is less concave on its lateral surface and the whole axis slightly less turned forwards at top and bottom, but these last two differences might disappear in more elderly animals. The ridge for the longitudinal digital flexor actually lies slightly further from the lateral edge of the bone than in *G. thomsoni* but perhaps not so far as in *G. granti*.

Phenacotragus is gazelline and not like the impala in having a tubercle on the top articular surface anterior to the attachments for the cruciate ligaments and ligaments from the menisci, and in having the longitudinal digital flexor ridge further from the medial edge of the posterior surface (but note the 1960 fossils on page 70). The shorter medial malleolus, although unlike living gazelles, is not likely to show relationship to the impala, and the other details of the distal end are as in living gazelles.

Metatarsal

There are two adult metatarsals (M.22464-65) which are from different individuals, one of them probably the same as that with the pelvic girdle M.22451, femora M.22452-53 and tibiae M.22454-55. There are also twelve juvenile specimens (six

of M.22428, three of M.22429, M.25035 and M.25037). The minimum number of individuals is nine or ten, which is also the minimum number for the herd.

They are not distinguishable from the Olduvai 1960 metatarsals, and are only doubtfully distinguishable from living gazelles by a proportionately larger naviculo-cuboid facet. Text-fig. 11 shows that the two adult bones fall beyond the range of living gazelles, but those of the younger individuals do not. The adult ones are relatively thicker than in living gazelles, as can be seen on Text-fig. 10, but not so thick as the 1960 metatarsals. They differ from *G. thomsoni*, but not so clearly from other gazelles, by having the top articular surface less upcurved at the front, and by having a lower back part of the top articular surface.

In the impala there is a slightly better marked longitudinal groove on the anterior surface, the ectocuneiform facet is not so upcurved in medial view, there is a short ridge bounding the medial side of the lateral extensor tendon at the top of the anterior surface and the anterior flanges just above the distal condyles are poorly developed.

Astragalus

There are eleven astragali (nine of M.22398, M.22457 and M.22461). It is more difficult to pair off right and left ones than it is with the long limb bones but the minimum number of individuals appears to be six. The range of variation is so great that reliable differences from gazelles are few. The excavation of the lower part of the lateral side is perhaps deeper than in living gazelles but not so deep as in the 1960 fossils from FLK and FLKN. They differ from both living gazelles and the 1960 fossils by having a narrower and sharper anterior rim on the top half of the lateral side.

Phenacotragus recki is undoubtedly gazelline and unlike the impala in the depth of the hollow on the lower lateral side, and in the lack of a deep indent on the lower posterior side.

The astragalus 1960 FLKN I, layer 3, 6253 may belong to *P. recki*.

Naviculo-cuboid

There are twelve naviculo-cuboids (six of M.22434, four of M.22435, M.22458 and M.22462). The minimum number of individuals is seven. They cannot be distinguished from living gazelles, but the posterior wall projects further backwards than in the 1960 fossils. They differ from the impala in that the outline of this posterior projection is not concave along its upper edge, in the lack of a hollow on the lower back part of the medial wall and in the lack of a facet to fit into the hollow on the posterior side of the astragalus. Since *P. recki* does not have the hollow on the astragalus the corresponding facet of the naviculo-cuboid is necessarily absent.

Scapula

The remains of six scapulae are found with the herd from SHK II; they are numbered M.22385, two of M.22386, M.22387, M.22442 and M.22443. The minimum number of individuals based on scapulae is four.

They cannot be satisfactorily distinguished from the 1960 fossils or from living gazelles, but it may be true that the medial side of the tuber scapulae is more concave (unless this is characteristic only of young animals).

Humerus

There is a pair of fully adult humeri (M.22404 and M.22406), a sub-adult one on which the epiphyses are closing (M.22444), four juvenile bones (three of M.22405 and M.22407), together with a distal end (M.22407). The minimum number of individuals is five and M.22444 probably came from the same individual as the pelvic girdle M.22451, the femora M.22452-53 and the tibiae M.22454-55.

They are not different from the 1960 fossils. The proximal end differs from living gazelles in having a protuberance on the floor of the bicipital groove in anterior view. The relative thickness of both the adult and the sub-adult humeri is greater than the mean value in *G. granti*, but only the adult one exceeds the mean for *G. thomsoni*.

The fossil agrees with gazelles and is unlike the impala in that the top of the greater tuberosity does not approach so closely to a horizontal position in anterior view, in the absence of a bony projection behind the infraspinatus insertion, in the absence of a ridge on the lateral side for the extensor carpi radialis origin and in the absence of a vertical ridge in the coronoid fossa above the distal condyles. The distal lateral groove may be less wide than in gazelles, but is a doubtful character difference.

Radius and ulna

There are nine radii from the SHK II herd. M.22410 and its olecranon M.22411 are fully adult and belong with the humeri M.22404 and M.22406. M.22445 and its olecranon M.22446 are sub-adult and go with the humerus M.22444. The other specimens (two of M.22388, M.22389, two of M.22408, two of M.22409 and two olecranons numbered M.22411) are all fragmentary or young ones. The minimum number of individuals is six. Text-fig. 12 includes a drawing of the proximal articular surface of M.22410.

In comparison with *G. thomsoni* the antero-medial edge of the medial facet at the proximal end is more evenly rounded; in comparison with *G. thomsoni* and other gazelles the lateral facet at the proximal end is more flattened, the top of the shaft shows a little less torsion on the lower part, the ridge forming the medial boundary of the scaphoid facet extends further ventrally and the extent of the cuneiform's articulation on the radius is greater. The lateral tubercle on the older radius is large and situated high as in living gazelles, on the younger sub-adult one it is smaller and low as in the impala. In the ratios of least thickness/length and length/length of humerus both the adult and sub-adult radii are less cursorially advanced than the means for *G. granti* and *G. thomsoni*. Three proximal ends from the 1960 dig, FLKN I 1217, unnumbered and 6106, can be assigned to *P. recki*.

The radius of *P. recki* is distinguished from the majority of the 1960 radii described above by the rounded edge of the medial facet at the top, the cuneiform's articula-

tion on the radius being greater, and possibly by the medial facet at the top being more indented posteriorly.

The impala agrees with *P. recki* in the flattened surface of the lateral facet, in having less torsion of the stem, the medial boundary of the scaphoid facet extending far ventrally, and the cuneiform's articulation on the radius being wide. But in other characters the impala is different from *Phenacotragus*; it has a hollow below the medial side of the medial facet, two forward projections of the medial facet, and distally that part of the scaphoid facet on the posterior surface is longer.

Metacarpal

There are four adult metacarpals—M.22412, M.22449-50 and M.25036. The middle two of them could be from the same sub-adult individual mentioned before, while the last is provisionally placed with the humeri M.22404 and 22406 and the radius M.22410. There are also five fragmentary or young metacarpals (M.22390, M.22413, two of M.22414 and M.22430). The minimum number of individuals represented is five. The proximal articular surface of M.25036 is illustrated in Text-fig. 12. The metacarpals from the three adult or sub-adult individuals are

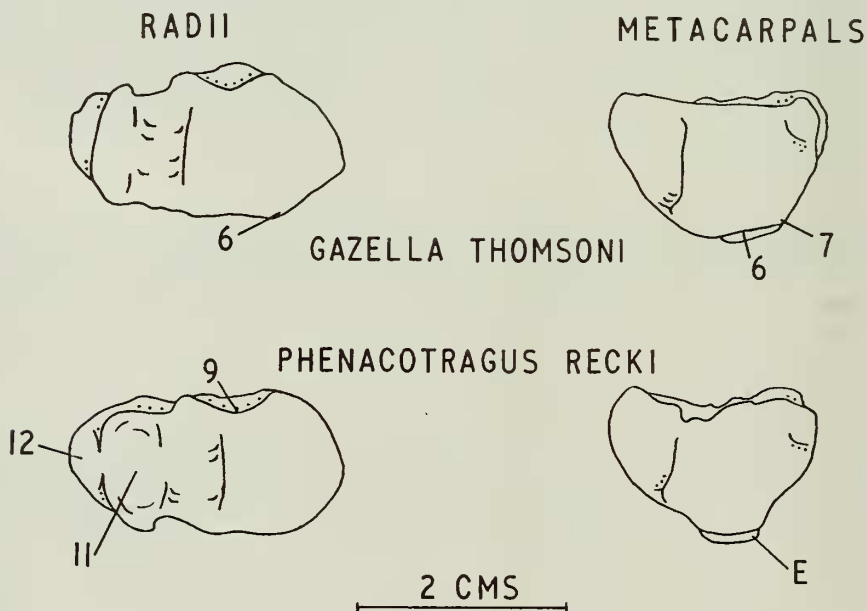


FIG. 12. Proximal articular surfaces of radii and metacarpals of *G. thomsoni* and *Phenacotragus*. The lateral side is on the left and the posterior side towards the top. On the metacarpals 7 shows the angled corner of the magnum-trapezoid facet and 6 the front edge of the facet with E, the extensor carpi radialis insertion, in front of it. On the radii 6 shows the antero-medial angle of the medial facet, 9 the posterior indentation of the medial facet, 11 the lateral facet, and 12 the lateral tubercle.

relatively thicker than in the measured living gazelles, and the fossils' mean for the ratio length of metacarpal/length of humerus is the same as that of the much larger *G. granti*.

They differ from living gazelles and from the 1960 fossils in having the extensor carpi radialis insertion more transversely compressed so that it is more localized and projects further anteriorly. The antero-medial side of the magnum-trapezoid facet is not so prominently angled as in *G. granti*, and the back edge of the top articular surface as a whole is more concave in M.25036. This last character is not the same as the more localized indentation mentioned as metacarpal character (2) in Gentry (in preparation). The proximal end FLKN I, 5149 from the 1960 dig and an unnumbered bone from FLKN I, trial trench, layer 3, may belong to *Phenacotragus recki*. The anterior proximal foramen is better developed than in living gazelles even in the adult fossil bones. Only one out of the four adult or nearly adult bones has an indented posterior edge of the top articular surface.

The impala differs from *P. recki* and living gazelles by having no anterior proximal foramen, a more deeply hollowed posterior side of the shaft, and the lateral end of the posterior edge of the magnum-trapezoid facet forming a backwardly pointed projection.

Phalanges

There are a large number of phalanges of *Phenacotragus recki* (M.22466-78). The first phalanges are like living gazelles, rather than the impala, in having two concave areas, one above the other, at the top of the posterior surface. However the flanges bounding the more distal of the concavities are less well developed than in gazelles, and this brings the appearance of the fossils somewhat closer to the impala.

Comparison of the limb bones of living gazelles, PHENACOTRAGUS RECKI and those from the 1960 dig in Bed I

Although the bones of *Phenacotragus* are more massively proportioned than those of living species, they are less massive than those of the 1960 dig in Bed I. This may be due to continuing skeletal evolution in the African Antilopini through the period represented by the basal part of Bed II; but part of the cause may be that the ontogenetic age of the two *Phenacotragus* individuals is less than the 1960 fossils or that the *Phenacotragus* may be females and the 1960 ones males.

The characters in which the fossils differ from living gazelles can be divided into three groups:

- A. Those in which the 1960 fossils and *Phenacotragus* agree.
 - B. Those in which the Bed II *Phenacotragus* is intermediate between the 1960 fossils and living gazelles.
 - C. Those in which the 1960 fossils or *Phenacotragus* are distinctive.
- A. The characters in this group possessed by the fossils are:
- (1) the shorter medial malleolus of the tibia;
 - (2) the flattened lateral facet of the radius;

- (3) the ventral extension of the medial side of the scaphoid facet at the distal end of the radius ;
- (4) perhaps a lesser torsion of the radius stem ;
- (5) the better developed anterior proximal foramen of the metacarpal.

B. Character differences from living gazelles in which the Bed II *Phenacotragus* is intermediate between the 1960 fossils and Recent species. The characters in this group are :

- (6) the degree of convexity of the distal lateral end of the femur ;
- (7) the course of the long digital flexor's ridge on the posterior surface of the tibia ;
- (8) the curving forwards of the long axis of the tibia at its top and bottom ends ;
- (9) the size of the naviculo-cuboid facet at the top of the metatarsal ;
- (10) the depth of excavation of the lower lateral side of the astragalus ;
- (11) the size and position of the lateral tubercle at the top of the radius ;
- (12) the indentation, or lack of it, on the posterior top edge of the metacarpal.

Many of these characters in the fossils are similar to *Aepyceros*, namely (1), (2), (3), (4), (6), (7), (9) and (11). In addition the deep hollow on the articular head of the femur of *Phenacotragus* and the shape of the posterior edge of the lower lateral side of the astragalus are not unlike *Aepyceros*. This might suggest that a relationship to that genus should be considered. However characters (1), (3), (6), (9), (10), (11) and perhaps (2) and (7) of the fossils are also like *Redunca* and *Kobus*, and characters (1), (4), (6), (7), (9) and (12) are like the Alcelaphini. Moreover characters (1), (4) and (9) at least may reasonably be taken to be more primitive in the fossils than in living gazelles. So the real situation is that the Olduvai fossils have a greater number of characters in common with other antelopes than have living gazelles.

However this is not the end of the story because a check at the British Museum (Natural History) on the limited number of limb bones assigned to the Pontian gazelles of Pikermi showed that they were like the Olduvai fossils only in characters (9) and perhaps (11). Two Pontian metacarpals were available for checking character (12) ; in one the posterior edge was indented and in the other it was not. In characters (2) and (3) the Pikermi radius is like those of living species, in (5) the two metacarpals are like *Aepyceros*, and in two astragali the excavation of the lower lateral side is less deep than in the Olduvai fossils but wider than in living gazelles (10). The state of the Pontian fossils was not satisfactorily ascertainable for characters (1), (4), (6), (7) and (8).

So while the conclusion from the African evidence alone could well be that the limb bones of the gazelline species at Olduvai were evolving towards the condition of living gazelles and away from a condition similar to the impala and to other tribes of antelopes, what there is of evidence from Pikermi does not fully support this conclusion. The fact that the lateral facet of the Pikermi gazelle's radius is not flat (2), that the medial side of the scaphoid facet is not extended ventrally (3), that the metacarpals lack an anterior proximal foramen (if this be not an age effect) (5), and that the excavation of the lower lateral side of the astragalus is no deeper

than in living gazelles (10), might all be evidence that the Pikermi species were not close to the ancestry of African living or fossil gazelline species. Or it might be true that they were close to the ancestry of living gazelles but not to that of East African gazelline fossils.

C. Characters possessed only by the 1960 fossils or by *Phenacotragus*. One or two characters of the 1960 fossils are distinctive, namely the less flattened posterior surface of the tibia, the lack of projection of the posterior wall of the naviculo-cuboid in medial view, and the possibly better developed unciform projection on the top articular surface of the metacarpal. The Bed II *Phenacotragus* is distinctive in the thinner anterior rim on the top of the lateral side of the astragalus (unless this is due to youthfulness), the wider cuneiform articulation on the radius and a transverse compression on the extensor carpi radialis insertion at the top of the metacarpal.

The Olduvai fossils are like the springbok only in the flatness of the lateral facet of the radius, the size and position of the lateral tubercle, perhaps in the length of the scaphoid projection distally, and in the short medial malleolus of the tibia. In addition the vertical ridge at the top of the femur 1960, FLKN I, 1027 is like the springbok. It cannot be said on the basis of these characters nor on the basis of those characters of the metacarpal and radius tops in which living gazelles are not uniform (antero-medial corner of magnum-trapezoid facet of the metacarpal, shape of antero-medial edge of the medial facet of the radius, shape of the side of the medial facet and indentation of the posterior side of the medial facet), that either the Bed I or Bed II fossils resemble *Antidorcas* more than *Gazella*.

VI. RELATIONSHIPS OF *PHENACOTRAGUS RECKI* (SCHWARZ) AND *GAZELLA WELLSI* COOKE

It was Schwarz's view (1937) that the Alcelaphini (hartebeests and wildebeests) should be included in the subfamily Antilopinae. According to him *Phenacotragus* could be placed between *Aepyceros*, the impala, and *Beatragus*⁹ as one of a trio of intermediate genera passing from gazelles to hartebeests and showing the reality of the relation between them.

The position maintained here involves changes of emphasis in Schwarz's views rather than their outright rejection. From its skull characters *Phenacotragus* is taken to be definitely gazelline and to have a close phyletic relationship or perhaps even a generic identity with *Antidorcas* of South Africa. *Aepyceros* is regarded as a somewhat isolated genus, certainly not like *Phenacotragus*, certainly not gazelline, and probably closer to the Alcelaphini than to any other group. Schwarz thus rightly pointed to the resemblances of *Aepyceros* and *Beatragus* as showing a relationship between them, but any resemblances found between *Aepyceros* and *Phenacotragus* would be, in my view, the result of chance, parallel evolution or of unchanged inheritance from a common ancestral condition. However it is possible that at a more remote level the Alcelaphini, or at least the hartebeests among them,

⁹ The Hunter's antelope or Tana River hartebeest—*Beatragus hunteri*—is the only species in this genus, which has occasionally been included in *Damaliscus*.

are related to the gazelline/caprine stock, and this involves a reappraisal towards Schwarz's views. Indeed it is further possible that *Phenacotragus* and *Antidorcas* could be closer to the hartebeest ancestry than *Gazella* itself, particularly since *Phenacotragus*, *Antidorcas* and the hartebeests¹⁰ are all limited to Africa whereas *Gazella* occurs also in Eurasia. But this is speculative as yet and it is only necessary here to show that phenetically *Phenacotragus* is gazelline and close to *Antidorcas*, that *Aepyceros* is very ungazelline, and that therefore the two are unlikely to be closely related.

Characters in which PHENACOTRAGUS differs from AEPYCEROS

The following differences in the skulls and teeth between *Aepyceros* and *Phenacotragus* can also be taken as separating *Aepyceros* from other gazelline genera.

1. The horn cores of the impala are unlike those of *Phenacotragus* in their wide divergence from the pedicel, in their long even curvature outwards and backwards, and in the abrupt turning inwards and forwards of the terminal portions. *Beatragus* has very similar horns, and those of *Alcelaphus* can be seen as a short, thickened version of the same basic shape.

2. The horn cores arise further behind the orbits in the impala than in *Phenacotragus*.

3. The supraorbital foramina are much wider apart in the impala than in *Phenacotragus*. This is an easily measurable character, and Text-fig. 13 shows the distance between the foramina expressed as a percentage of the orbital width in some selected

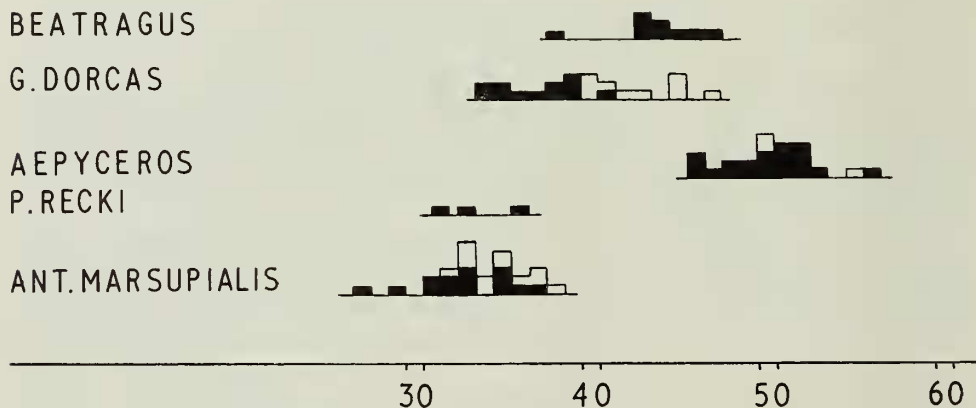


FIG. 13. Histogram of width of supraorbital foramina/orbital width. $\times 100$. Unblackened readings indicate females and blackened ones males, but the sexes of *Beatragus hunteri* and the *Phenacotragus* were not determined. *Phenacotragus* is clearly most like *Antidorcas marsupialis* in this ratio. Ten of each sex of *G. dorcas* were measured, and the females had the supraorbital foramina wider apart than in the males.

¹⁰ One hartebeest is known from the Lower Pleistocene of India (Pilgrim 1939 : 67), doubtless a wanderer from Africa.

antelope genera. In *Phenacotragus* and the springbok the foramina are very close together and there is no overlap with the impala. The readings for *Gazella dorcas*, as a representative gazelle, and for *Beatragus* are intermediate. The supraorbital foramina are situated further forwards from the base of the horn pedicels in the impala, and this also helps to give this region of the skull a quite different appearance from any gazelline species.

4. The braincase of *Phenacotragus* (M.21460) looks a little shorter than in the living *Gazella rufifrons*, which means that it is certainly shorter than in most other gazelles, but the braincase of the impala is still shorter than in *Phenacotragus* or any gazelline species.

The facial region of the impala is lengthened and the back edge of the tooth row in adults lies further forwards relative to the orbits than in the type skull of *Phenacotragus*. There is a size allometry for this character in gazelles with bigger species having the tooth row further forwards, but the tooth row of the impala is still further forwards than in the largest gazelles. The long face of the impala cannot safely be regarded as a separate character from its short braincase, because both may be only consequences of more posteriorly situated orbits. It is likely that mechanical factors and questions of support are involved here, since there does seem to be a relation between the two dimensions among the Alcelaphini, Antilopini and Caprinae, with *G. thomsoni* and *Alcelaphus* species at opposite extremes among living forms.

5. The anterior tuberosities on the basioccipital of the impala are close together as in *Phenacotragus*, but their shape is different and there are strongly marked longitudinal ridges behind them.

6. The walls of the central cavities on the occlusal surfaces of the upper molars have anterior and posterior localized infoldings in the impala but not in *Phenacotragus*. The impala also shows a greater curvature of each central cavity in the unworn state (see Text-fig. 14). These are not characters which would allow certain identification of isolated teeth, but they are consistent and recognizable in series of teeth. Among gazelline genera only *Antilope* has much tendency towards similar infoldings but the shape of its central cavities as a whole is different from either *Aepyceros* or other gazelline genera.

7. The medial walls of the anterior and posterior lobes of the lower molar teeth are more convex in the impala, and the lateral walls of the lobes too are more evenly rounded and less acutely pointed than in living gazelles or *Phenacotragus*. The central cavities on the lower molars are distinctively shaped with more transverse constriction of their mid-points than at either end (see Text-fig. 15). The lower teeth of *Antilope* and the lower teeth in the British Museum (Natural History) supposedly of *Helicotragus* and *Gazella mytilinii*, are similar to *Aepyceros*. The lower molars of *Phenacotragus* are at the opposite extreme with their fairly straight medial walls. The functional meaning of the diverse patterns of lower molars in antelopes is not understood, nor to what extent there is a necessary correlation between the complicated folding of the walls of the central cavities of the upper molars and the varying characters of the lower molars. The combination of upper and lower molars similar

to *Aepyceros* in *Antilope* suggests some correlation. In any event, the pattern of dental evolution is very different in *Phenacotragus* and *Aepyceros*.

8. The medial wall of P_4 in the impala has the anterior valley closed off, i.e. the valley has become an internal cavity and the wall bounding it is complete. This is unlike any gazelline species except the Asiatic *G. gutturosa*, *G. picticaudata* and *G. sinensis*, but it is found in all living Caprine and Alcelaphine genera.

9. The ramus of the lower jaw of the impala is rather shallower than in *Phenacotragus* or other gazelline species and the ascending ramus slopes more.

In all the characters listed above the impala is not only unlike *Phenacotragus* but shows slight resemblances to the Alcelaphini—more than does any gazelline genus. Also unlike Antilopini but like the Alcelaphini is the fact that the median indentation at the back of the palate in the impala projects further anteriorly than the lateral indentations. The impala obviously lacks the extreme skull specializations of *Alcelaphus* and *Damaliscus*, and except for the similarity of its horns to those of *Beatragus* there is no reason to suppose it is particularly closely related to them. Fossil finds of the Alcelaphine faunas of earlier periods in Africa may help to close the gap. Other differences between impala and *Phenacotragus* skulls are indecisive in assessing relationship, e.g. the larger auditory bulla of the impala, its loss of a preorbital fossa and its reduced ethmoidal fissure. The size of the bulla can differ even in closely related antelopes, and the last two characters are known to show parallel changes in different lineages. The presence of a long foramen between the premaxilla and maxilla in the impala and the strong lateral flanges on the front of its nasals are probably a peculiarity of the species, different from either Antilopini or Alcelaphini.

Only three firm similarities can be found in the skulls of *Phenacotragus* and the impala. These are :

1. the high level of the frontals between the horn pedicels compared with the level of the orbital rims ;
2. the long nasals ;
3. reduction in the size of P_2 .

All three characters are also shared in common between *Phenacotragus* and the springbok. In the high level of its frontals *Phenacotragus* looks much more like the springbok and not at all like the impala ; the many other differences in this region of the skull quite overshadow the effect of this one resemblance to the impala. The nasals of *Phenacotragus* are so narrow as to remind one of a hartebeest or a reduncine, and are not very like those of the impala in anything other than being narrower than in gazelles ; nor in fact are they very much like the springbok.

In writing that *Aepyceros*, *Phenacotragus* and *Beatragus* were genera which seemed to show the connection between the gazelle and hartebeest groups, Schwarz was not very precise, but if his view were true, presumably one ought to be able to see a number of characters in common, or even gradations of characters, between the hartebeest and the gazelle extremes. In fact this expectation has not been fulfilled. While the impala shows tendencies towards the characters of the Alcelaphini,

Phenacotragus shows no positive likeness whatever to the impala. There is a sharp break along this line from gazelles to hartebeests, whatever may be the case with undiscovered fossils.

It is because of the slight but definite alcelaphine tendencies in the skull of the impala and the total absence of convincing resemblances to gazelles that it cannot be thought of as simply a rather aberrant or even the most aberrant known gazelline genus. In addition its limb bones have an unusually high number of distinctive characters, very few of which are shared by *Phenacotragus*, and show a high total of character differences from gazelles. It is evident that the skeletal adaptations for pronking (a jumping gait) in the springbok (and those for stotting in gazelles?) are quite different from those for leaping high in the impala. As in its teeth, so too in its limb bones, morphological adaptation has evolved along different lines. One can only regard the impala as the successful occupant of an ecological niche rather remote from any others, and I think it may best be classified by being included in the tribe Alcelaphini. A fossil horn core 1957, BK II, 662 shows the presence of *Aepyceros* in the upper Bed II fauna of Olduvai, and Arambourg (1947) records it from Omo.

Characters in which PHENACOTRAGUS agrees with ANTIDORCUS MARSUPIALIS

After rejection of the postulated relationship of *Phenacotragus* and the impala, the alternative choice for the genus most nearly related to *Phenacotragus* falls on *Antidorcas*. The springbok agrees with *Phenacotragus* in the following skull characters.

1. The details of the shape and insertion of the male horn cores. Those of the springbok have no lateral flattened surface, are bent backwards and outwards, sometimes have the same slight tendency towards spiralization as in *P. recki*, and often have transverse ridges on their lower parts. Similar horns are found in *G. dama* of West Africa, but this species has large supraorbital pits and a long pre-molar row and is clearly not closely related to *Phenacotragus* or the springbok. Springbok horn cores are, however, less laterally compressed than in *Phenacotragus* or *G. wellsi*.

2. The supraorbital foramina of the springbok (Pl. 9B) and *Phenacotragus* are not set widely apart, as can be seen in Text-fig. 13 where the readings for the two genera are identical. This, combined with the high level of the frontals between the horn pedicels, gives a very similar appearance to this region of the skull.

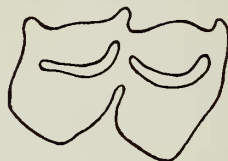
3. The braincases of the springbok and *P. recki* are both somewhat shorter than in most gazelles. This is likely to be an advanced condition, but it has not been carried to the extreme seen in the impala.

4. In the springbok the descending flanges of the basisphenoid have their origin further back relative to the foramina ovals than in gazelles. Enough has been preserved of the fossil basioccipital piece M.22371 to show the descending flanges starting as far back as in the springbok, while in the skull M.21464 the flanges are

ANT. MARSUPIALIS



GAZELLA GRANTI



PHENACOTRAGUS RECKI



AEPYCEROS



1 CM.

FIG. 14. Occlusal views of upper molar teeth. The lateral side is towards the top of the page and the anterior side towards the right. The *Phenacotragus* tooth is drawn from M.21464.

ANT. MARSUPIALIS.



GAZELLA GRANTI



PHENACOTRAGUS RECKI



AEPYCEROS



1 CM.

FIG. 15. Occlusal views of lower molar teeth. The medial side is towards the top of the page and the anterior side towards the right. The *Phenacotragus* tooth is drawn from M.22436.

slightly more anterior but still nearer to the springbok position than to that of gazelles; M.21460 appears to be more like a gazelle. The basisphenoid flanges of the impala descend less sharply than in Antilopini (although the difference from M.21460 does not seem pronounced), and arise anteriorly to the foramina ovals.

5. The shape of the lower jaw's horizontal ramus in the springbok (Pl. 9C) and *Phenacotragus* is different from either gazelles or the impala. That of gazelles becomes progressively more shallow from the back forwards but there is no sharp change of direction of the lower edge as seen in profile; males often seem to be relatively deeper under the premolars, but the difference from females was not found to be statistically significant. Passing forwards in *Phenacotragus* and the springbok the lower edge is at first very deep under the back molars, then changes direction sharply to rise under the premolars. Such a posteriorly deepened ramus is presumably necessary to house the hypsodont teeth and is dissimilar to the ramus shape of gazelles. *Phenacotragus* and the springbok also have an indentation of the lower edge of the ramus just behind the point where it changes direction. The impala has a slight bending of the course of the lower edge of its ramus, but is not so deep under the molars as in *Phenacotragus* or the springbok.

6. The lower molars of the springbok differ from gazelles in the straighter outline of their medial walls and in a more pronounced inturning of their anterior end. The central cavities are also sometimes straighter. *Phenacotragus* with the straighter medial walls of its lower molars but without such noticeably straight central cavities could easily be showing an earlier stage in the development of springbok-like teeth.

7. The upper molars of *Phenacotragus* differ from gazelles in having more prominent styles and in the more marked concavity of the posterior part of their lateral walls. The springbok is intermediate between gazelles and *Phenacotragus* in these characters. Individual teeth of the springbok could often not be told from those of gazelles, but a series from the springbok can be seen to be similar to *Phenacotragus*. (Upper molars of the impala may sometimes have a better developed mesostyle than gazelles, but only rarely have a concave posterior wall.)

8. The premolar row of *P. recki* is probably more reduced than in living gazelles, although it may not be so close to the springbok for this character as is *Gazella wellsi*. Since the impala also has a short premolar row, this character can only be used for indicating resemblance to the springbok if the other evidence for separating *Phenacotragus* from the impala is considered satisfactory.

9. A more uncertain resemblance of *P. recki* to the springbok is that in both animals the palatal foramina may be positioned rather more posteriorly than in gazelles. This is found in many individuals of the springbok and also in the cast of the type skull of *P. recki*.

10. The auditory bullae of both *P. recki* and the springbok are smaller than in gazelles or the impala. Although this may be a valid point of resemblance between them, it is also true that the size of the bulla can vary greatly, even in closely similar forms. Hence the propriety of using it here is doubtful.

It is helpful at this point to tabulate how the teeth of *Aepyceros*, *Antidorcas* and *Phenacotragus* differ.

	<i>Aepyceros</i>	<i>Phenacotragus</i>	<i>Antidorcas</i>
Styles on upper molars	perhaps better marked than in <i>Gazella</i>	better marked than in <i>Gazella</i>	perhaps better marked than in <i>Gazella</i>
Concave posterior part of outside wall of upper molars	rarely present	usually present	sometimes present
Tendency towards a complicated folding of the enamel walls of the central cavities of the upper molars	tendency present	less apparent	less apparent
Curvature of unworn central cavities of upper molars	better marked than in <i>Gazella</i>	as in <i>Gazella</i>	as in <i>Gazella</i>
Closed anterior valley of medial wall of P ₄	present	absent	absent
Medial wall of lobes of lower molars	outwardly bowed	± straight	± straight
Central cavities of lower molars	constricted in the middle	as in <i>Gazella</i>	sometimes straighter than in <i>Gazella</i>
Reduction of premolars	little reduced	reduced	very reduced

The sign ± means more or less.

Few differences could be found between the skulls of *Phenacotragus* and the springbok. It is likely that the nasals of the springbok are relatively wider and that their posterior suture with the frontals has a more nearly transverse course. No complete nasal bone of *Phenacotragus* exists to provide decisive evidence on the first point, but, on the second point, the type skull, the frontlet M.21462 and the isolated nasal bone are all constant. The ethmoidal fissure of the springbok is very small or absent, being reduced at least as much as in *G. thomsoni*; the preorbital fossa is smaller than in *Phenacotragus recki*.

The horns of springbok males are less laterally compressed than in *Phenacotragus*; those of females are generally thin along their entire length and not greatly thickened at the base, but they are perhaps less reduced than in living gazelles, and in this they are nearer to *Phenacotragus*.

The back of the basisphenoid of *P. recki* is not so wide as in the springbok, and this is linked with the two species having dissimilar anterior tuberosities of the basioccipital. In connection with the basioccipital differences it may be noted that the cranium M.21463 (p. 58) has tuberosities not unlike either genus.

The hollow behind the maxillary flanges on the palate of *P. recki* is less deep than in the springbok.

The ascending ramus of the lower jaw of the springbok is taller than in *Phenacotragus*. In the teeth the outside wall of the posterior lobe of the upper molars in *Phenacotragus* is more concave than is usual in the springbok and the central cavities of the lower molars are not quite so straight antero-posteriorly. Both these tooth differences are minor and it should be remembered that in both genera the teeth vary in the same direction from gazelles as shown in the summary table above.

The limb bones of *Phenacotragus*, springbok and gazelles are all very much alike, and it cannot be held that *Phenacotragus* and the springbok show any closer similarities than either does to gazelles.

As there is no doubt of the close phenetic similarity of *Phenacotragus recki* to the springbok, the question arises of whether *Phenacotragus* should be dropped as a generic name in favour of *Antidorcas*. The case for this is quite strong, and in some characters *P. recki* is even suitable as an ancestor for *Antidorcas marsupialis*. Its premolar row is not so shortened as in the living species, P_2 is still present in the few available adult mandibles and P_3 is not very much reduced. The central cavities of the lower molars are not so straight as they may be in the springbok; neither the preorbital fossa nor the ethmoidal fissure are so small. The basioccipital of *P. recki* has presumably evolved from a condition similar to that of the Pontian *Gazella capricornis*, and its anterior tuberosities could surely have evolved further to the state in which they are found in the springbok. However *P. recki* is difficult to visualize as a possible ancestor of the springbok in the characters of the outside walls of its upper molars, the shape of the back of its nasals and the horn cores of the females, but this of course need be no bar to uniting the genera.

One or two other considerations, however, suggest to me the need for caution at least for the present. Firstly there is the existence of a second species of *Phenacotragus*, namely *P. vanhoepeni* from Makapansgat in South Africa (Wells & Cooke 1956), of which there is a frontlet (M.16732) and a horn core (M.16715) in the British Museum (Natural History). Its horn cores are more massive than in *P. recki*, they seem to rise more steeply from the frontals, the lower part is longer before the horn core curves backwards and the lateral surface is flattened. They are also much more laterally compressed than in *P. recki*, and the frontals between the horn cores are not at a higher level than the orbits. The illustration of the basioccipitals shows anterior tuberosities apparently less unlike *Gazella dorcas* or *G. granti* than those of *P. recki* are. Clearly, *P. vanhoepeni* is less like the springbok than is the East African *Phenacotragus*. One could easily postulate that *P. vanhoepeni* had diverged more from the supposed central stock than had *P. recki*, but this is to wander away from available evidence.

Secondly there is the appearance of characters reminiscent of *Antidorcas* in other fossil gazelline species at Olduvai. In *G. wellsi* the supraorbital pits are very small and the frontals between the horn bases are at a higher level than the orbital rims, the horn cores are bent backwards, the premolar rows are shorter than in living gazelles and P_2 is even sometimes absent. The gazelline cranium (M.21463), which was a surface find from FLK II in 1935 (see p. 58), is not distinguishable from the *G. wellsi* of Bed I, and has a basioccipital which is morphologically intermediate between *Phenacotragus* and *Antidorcas*. Among the limb bones from the 1960 excavations the slight vertical ridge on the anterior surface of the femur FLKN I, 1027 is the most striking springbok-like character.

Several explanations are possible for these phenomena and it is evident that the phyletic relationships between the springbok, the two species of *Phenacotragus*,

Gazella wellsi and other gazelles are not yet clear. It is advisable to consider what may be the far-reaching implications of some of the skull characters of these East African fossils. It is particularly characteristic of the genus *Gazella*, as far back as in the Pontian species of *Attica*, to have a low level of the frontals between the horn cores' bases. This condition is also found in the related genera *Oioceros*, *Helicotragus*, *Antilope*, *Litocranius* and *Ammodorcas*, and in some Bovid tribes other than the Antilopini, e.g. the Neotragini and Reduncini. *Antidorcas*, *Gazella wellsi*, *Phenacotragus recki* but not *P. vanhoepeni* show the opposite condition of high level frontals coupled with supraorbital pits which are either small or absent, and which even when present lack the characteristic gazelline triangular shape. Such characters do not occur in Eurasian fossil gazelles or even in those described from the Algerian upper Pleistocene.

If the African forms are descended from typical gazelles, then their high frontals and small supraorbital pits are a relatively late evolution, and they might best be classified by retaining *G. wellsi* within *Gazella*, and by separating the other two as *Antidorcas* and *Phenacotragus* if they are two different and parallel divergences from this stock, or by putting them both in *Antidorcas* if they are the products of only one such divergence. But it is still not known even that the two *Phenacotragus* species are closer to one another than to the other forms, nor can it be assumed that *Gazella wellsi* is phenetically or phyletically further from the springbok than *Phenacotragus* is.

If, on the other hand, the Pliocene and earlier ancestors of these African forms also possessed high frontals and small non-triangular supraorbital pits, their relationship to typical *Gazella* is more distant. It may well be that a predominantly grazing "Antidorcine" group of Antilopini has long inhabited Africa, existing alongside typical gazelles such as are represented at Olduvai by the horn cores SHK II 285, BK II 226 and M.14508 (see above), and that the springbok of South Africa is the only survivor of this formerly more widespread and diverse stock. Further finds at Olduvai and at other East African sites may give more information about this interesting possibility. If evidence were found in support of it, then the problem of classification might be dealt with by placing *G. wellsi*, *Phenacotragus* and *A. marsupialis* all in the genus *Antidorcas*.

A third still more hypothetical possibility is that the springbok, *Phenacotragus* species and *G. wellsi* are a gazelline-like development from the hartebeest group—a possibility which would much weaken the idea of even a remote relationship of the hartebeest group to the gazelline-caprine stock. If it were true the problems of generic differentiation would remain, but within a different tribe. In the absence of evidence for one of these three evolutionary histories, it is best to retain the existing name *Phenacotragus* and to refrain from moving *G. wellsi* to another genus. Under this arrangement the genus *Phenacotragus* differs from *Gazella wellsi* by having horn cores which are longer, less divergent proximally but outwardly divergent in their distal parts, and a concave outer wall of the posterior lobe of the upper molars. The flattened lateral surface of the horn cores, available as a character in East Africa to distinguish *P. recki* from *G. wellsi*, is not available in this broader context because of the flattened lateral surface of *P. vanhoepeni* horn cores.

It may be useful at this point to summarize the contrasts in skull evolution in *Phenacotragus*, *Antidorcas* and "normal" gazelles. *P. recki* and *Antidorcas* have a high level of the frontals between the horn bases and small supraorbital pits, and the descending flanges of the basisphenoid originate more posteriorly relative to the foramina ovals. They are advanced from Pontian gazelles in having shortened braincases (but note the less marked tendency towards shorter braincases in *Gazella rufifrons* and *G. soemmerringi*), better developed styles on the upper molars, straighter medial walls of the lower molars, the posterior deepening of the mandible, and the reduced premolar row. But they have retained rather long nasals, they have little transverse compression of the horn cores, and the horn cores of females are often less reduced than in gazelles.

The living African gazelle which shows the most extreme differences from the springbok and *Phenacotragus* is *G. thomsoni*. Admittedly *G. thomsoni* has a reduced premolar row, but even here there is slender evidence (Gentry 1964) for supposing that *G. thomsoni* reduces the back of its premolar row rather than P_2 .

Some of the skull characters of *Gazella wellsi*, *Phenacotragus* and *Antidorcas* in Africa are paralleled in the Caprinae of Eurasia. Such characters are the shorter braincase than in most gazelles, the high level of the frontals and the strong development of the central anterior flanges of the nasals, which are all carried to a further extreme in *Capra* and *Ovis*. The shallowness of the mandible under the premolars in *Antidorcas* and *Phenacotragus*, the development of the styles on the upper molars of *Phenacotragus*, and the possibly prominent metastyle of M^3 in *G. wellsi* are also approaches to the caprine condition. P_2 has disappeared in *Saiga* on the steppes of Asia as in the African species, but the advanced structure of P_4 , found in the *Procapra* group and Caprinae, is unknown in any African gazelline species.

VII. SUMMARY AND CONCLUSIONS ABOUT THE GAZELLINE FAUNA OF OLDUVAI

The introduction to this work contains revised definitions of the Antilopini, *Gazella* and *Antidorcas marsupialis*, together with a discussion of some tooth characters of gazelles. The remainder is about the gazelline fauna of Beds I and II at Olduvai so far as it is known, and the chief point of interest is its marked difference from the fauna now living in East Africa. Today there are the smaller *Gazella thomsoni*, the larger *G. granti*, and *Litocranius*; then there were *G. wellsi*, *Phenacotragus recki* and several others.

Phenacotragus recki is more nearly related to the extant South African springbok than to present day East African forms, as is shown by the shape and insertion of the horn cores, the size of the supraorbital foramina, the high level of the frontals between the horn bases, the short braincase, the probably rearward position of the descending flange of the basisphenoid, the shape of the mandible, and by certain details of tooth structure and proportion.

Gazella wellsi similarly shows certain resemblances to the springbok, and until the relations between this form, *P. recki*, the South African fossil *P. vanhoepeni* and the

springbok can be seen more clearly it is inadvisable to alter the existing formal nomenclature.

While *P. recki* and *G. wellsi* appear from their advanced teeth to have been predominantly grazing forms, there are a further three or more gazelline species from Olduvai, which may have included browsing forms. They are incompletely preserved, and at least two of them appear to belong to *Gazella*. Only the horn core (M.14508) is at all like the living species. It is not yet clear how many of the fossil species would have occurred together at any one time.

P. recki does not appear to have any convincing resemblances to the impala, although Schwarz (1937) thought that it did, and I believe that the genus *Aepyceros* should be removed from the Antilopini and added to the Alcelaphini.

The gazelline limb bones from Bed I show less fully cursorial proportions than in any comparable living African form.

There are no fossil remains referable or related to *Litocranius*, and none shows such brachyodont teeth or such a shallow jaw ramus. The ancestry of *Litocranius* is unknown, it is so specialized in several respects for browsing that it may have come from less brachyodont ancestors.

There are no recognizable remains at Olduvai of the spiral-horned genera of the *Helicotragus-Antilope* group. The nearest record is at Bethlehem where Hooijer (1958) has found *Gazellospira torticornis*.

APPENDIX I

The method of referring teeth to certain age states which has been followed in this paper is that of Brooks (1961: 132); his definitions of the relevant age states are:

- VII. Milk premolars lost; permanent premolars fully erupted but not worn; third molar fully erupted.
- VIII. First molar slightly worn, still with centre crest and sulci deeply cleft and V-shaped.
- IX. First molar without centre crest, sulci crescent shaped; third molar crested with V-shaped sulci.
- X. First molar worn, surface smooth with no vestige of sulci; third molar moderately worn, with crescent shaped sulci.

Measurements mentioned in this paper were taken on all suitable fossils, and on Recent specimens in age states VIII and IX as defined immediately above, that is on young adults. The measurements were:

- antero-posterior diameter of horn pedicel the longest dimension of the pedicel, irrespective of whether it was parallel to the long axis of the skull;
- transverse diameter of the horn pedicel the measurement at right angles to the antero-posterior diameter. These first two dimensions were taken on the pedicels rather than the horn cores because the sheaths of Recent species in museum collections are often irremovable;

length M ¹ -M ³		the maximum length at crown level ;
length M ²		the maximum length at crown level ;
length P ² -P ⁴		from the centre of the posterior wall of P ⁴ to the anterior wall of P ² , irrespective of whether the occlusional surface extends as far as the anteriormost point ;
length P ²		from the centre of its posterior wall to the anterior wall, irrespective of whether the occlusional surface extends as far as the anteriormost point ;
parieto-occipital angle		measured with a carpenters' sliding bevel ;
braincase width		the widest possible dimension ;
orbital width		the widest possible measurement across the posterior side of the orbits ;
separation of horn cores		the distance apart of the closest points of the lateral sides of the horn pedicels ;
separation of supraorbital foramina		taken between the central points of the lateral walls.

The measurements on the fossils, expressed in centimetres unless otherwise stated, were :

<i>Phenacotragus recki</i> (Schwarz)							
	Age state	Antero-posterior diam. of horn pedicel	Transverse diam. of horn pedicel	Length M ¹ -M ³	Length M ²	Length P ² -P ⁴	Length P ²
M.21460	IX	3.72	2.58	4.03	1.43	2.39	0.77
M.21462	—	3.26	2.34	—	—	—	—
M.21464	VII	2.85	2.14	3.71	1.45	2.06	—
1960, FLKN I, 627	VIII	—	—	3.83	1.38	1.85	0.53
<i>Gazella wellsi</i> Cooke							
1960, FLKN I, 6334	X	2.85*	2.12*	3.73	1.26	2.87	0.55
1960, FLKN I, 1152	IX	—	—	3.72	1.27	1.79	0.57
1960, FLKN I, 1662	X	—	—	4.62	1.56	2.27	0.75

* Not used in the histogram on Text-fig. 8.

Other horn cores placed with *Gazella wellsi* had the following dimensions :

1960, FLK I, G.13, 229	3.02 × 2.19	1941, F.944	2.92 × 2.14
M.22360	3.61 × 2.25	M.22363	3.18 × 2.38
1941, F.939	3.43 × 2.71	1941, F.940	3.08 × 2.15

Those of group (A) measured :

1959, KK I, 309	3.03×1.91	M.14512	2.87×1.88
1959, HWK II, 472	2.33×1.56 (the supposed female).		

1953, SHK II, 285 in *Gazella* species of group (B) measured 2.82×2.31 .

M.14508, group (F), measured 2.64×2.00 .

Other measurements of length of M²s in specimens assigned to *Gazella wellsi* were 1.16, 1.23, 1.10 and 1.30. 1960, FLKN I, 122, placed with *Phenacotragus recki*, is a molar tooth 1.54 cm. long ; it is assumed to be an M².

Other measurements on the skulls of *P. recki* were :

	Parieto-occipital angle	Braincase width	Orbital width	Separation of horn cores	Separation of supra-orbital foramina
M.21460	132°	6.45	9.46	—	2.98
M.21462	—	—	9.20	6.13	3.00
M.21464	132°	5.17	8.52	5.90	3.06

Measurements of length and least thickness were taken on limb bones of the following species :

	Males	Females	Sex unknown	Young or juvenile
<i>Aepyceros melampus</i>	3	2	—	2 (male and female)
<i>Antidorcas marsupialis</i>	1	1	—	—
<i>Gazella dorcas</i>	1	—	2	—
<i>Gazella thomsoni</i>	3	2	1	1 (male)
<i>Gazella granti</i>	6	4	1	—

The readings for young animals have not been entered on the histograms in Text-figs. 9, 10 ; they had relatively longer metapodials and shorter radii and tibiae than the adults. All the front leg bones were thinner than in adults except for the radius of the juvenile *G. thomsoni*, but in the back legs the differences from adults were less marked and not reliable.

The lengths of the limb bones were measured as follows :

femur : from the lateral end of the articular head to the ventralmost level of the posterior part of the medial condyle ;

tibia : from the ventralmost point of the medial facet at the top to the posterior tip of the bone behind the medial malleolus ;

metatarsal : from the highest point of the bone behind the ectocuneiform facet medially to the articular surface on the medial side of the most projecting part of the medial condyle distally ;

humerus : from the top of the greater tuberosity to the ventralmost point of the medial side distally ;

radius : from the medialmost point of the medial facet to the most distal point of the ridge bounding the scaphoid facet medially ;

metacarpal : from the anterior edge of the articular facet at the extensor carpi radialis insertion to the articular surface on the median side of the most projecting part of the medial condyle distally.

APPENDIX II

Excavations at Laetolil near Olduvai in 1935 and 1959 have yielded fragments of apparently gazelline horn cores and teeth, most of which differ from Olduvai remains. Specimens M.22483, three of M.22484, M.22491 and M.22494 are horn cores of almost circular cross section, two specimens numbered M.22484 are smaller than the others and may be females ; it may be that these Laetolil finds represent large Neotragini, but two left horn cores in Nairobi, 1959, 46 and 50, are more like a small species of *Gazella*. M.15110, M.22485, two of M.22486, two of M.22487, three of M.22488, M.22492 and M.22495 are all mandible fragments which are very shallow below the teeth ; 1959, 298 and 603 at Nairobi are also of this group. The distal end of humerus (M.22489) may go with the largest group of horn cores and mandibles, as may also two astragali, 1959, 19 and 328 at the National Museum in Nairobi. These astragali, together with Olduvai, 1959, MTK I, 104 have a shallow excavation on the lower part of the lateral side.

Also from Laetolil is a mandible fragment, 1959, 54, which has a deeper ramus than those mentioned above, although its teeth seem identical. A large gazelline species is represented by 1959, 150, 151, 294 and 443 + 444 and by one of the pieces numbered M.22487 in the British Museum (Natural History). These are all mandible fragments or lower teeth, perhaps from a large species of *Phenacotragus* judging by the relatively straight medial walls of the teeth.

The 1964 excavations at Lake Natron have revealed fragments of a large *Phenacotragus* represented by the maxilla WN 64, 300B, and a small *Phenacotragus* represented by the horn cores WN 64, 113, the mandibles WN 64, 95, 152, 241 and 291, and possibly by the limb bones WN 64, 79 and 213. Also from the Lake Natron beds are the horn cores WN 64, 75 and 126 which might be the same as the Laetolil *Gazella* 1959, 46 and 50. Isaac (1965) gives details of the Natron beds.

A gazelline horn core (M.15883) from Kanam West is like M.14508 from Olduvai (p. 67) in size and in its index of lateral compression at 76 (see Text-fig. 8). It differs from M.14508 in having a narrower section anteriorly, that is by having its level of maximum width further back and more localized ; this may be a slight feature morphologically but it does give M.15883 an appearance very like that of modern gazelles. In their three characters of size, lateral compression, and shape of cross-section, the two fossil horn cores agree with *G. rufifrons* among living species.

Those of *G. dorcas* are smaller and have the level of maximum width still further back; in *G. spekei* they are smaller and have pronounced lateral compression; those of *G. thomsoni* are nearer in size but again have much lateral compression; while those of *G. rufifrons* are similar in size and shape and are only slightly more compressed. Without more finds of this fossil animal, one cannot know whether it is related to a living gazelle or whether the resemblances to *G. rufifrons* are a matter of chance.

Two horn cores from Kanjera (M.15851) and one from Aringo Karungu (M.22502) are very like *G. granti* in both size and extent of lateral compression.

APPENDIX III

Leakey (1965) has given a preliminary report on the Olduvai gazelline species. He considers that Schwarz's species *Gazella gazella praecursor* may be represented in the British Museum's Olduvai collection by the horn cores M.14507 and M.14508 on account of their likeness to *G. thomsoni*—the species to which *G. g. praecursor* was supposed to be the forerunner. I have placed M.14507 with the *Gazella* species (B) of this paper but agree that M.14508 is similar to *G. thomsoni* despite its having less transverse compression than that species.

Leakey's species (a), the 1935 herd excavated from SHK II, is also here taken to be *Phenacotragus*, and I have been unable to separate it satisfactorily from *P. recki*.

The horn core (b) which is said to have "certain resemblances to the horn cores of the so-called 'Mongolian gazelle'", I believe to belong to a small *Damaliscus* or to a genus closely related to *Damaliscus*.

(c) The horn core (M.14513) is one of those which I have determined, perhaps rashly, to be females of *Phenacotragus* as explained earlier in this paper. Leakey's description of his species (c) fits the horn cores belonging to group (A) of this paper, one of which is numbered M.14512.

(d) The skull figured by Leakey (1965, pl. 85) is M.21463, a surface find from FLK II which seems to be *G. wellsi*.

(f) The frontlet 1955 BK II East, surface find no. 7 is a lightly fossilized young *G. granti*, or *G. cf. granti* according to Leakey. The entry in the record of excavations for 1955 reads: "Pair of horn cores and frontlets, surface above Bed III? from V on condition. in two parts". From this it seems unlikely that the frontlet belongs to a Bed II fauna.

The specimens listed under the headings (g), (h) and (i) are all taken here as belonging to *G. wellsi*, and have been considered earlier in the paper.

(j) The horn cores figured by Leakey (1965, pl. 86) might be Antilopini as he suggests, but more complete remains of such surprising animals are needed for a reliable assignment.

The horn core (M.14563) which Leakey (1965: 65) records as *Phenacotragus recki* is here taken to be a later occurrence of *G. wellsi*.

The impala-like horn core 1957, BK II, 662 mentioned by Leakey also seems to me good evidence of the presence of *Aepyceros* in upper Bed II.

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